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Economically Important Diseases of Lettuce

Lettuce (*Lactuca sativa* L.) is an economically important crop grown worldwide. California leads the United States in lettuce production—about 67,000 ha planted per year for a crop valued at approximately $265 million. Lettuce is also produced in Alaska, Arizona, Colorado, Florida, Hawaii, New Jersey, New Mexico, New York, Texas, and Wisconsin. Because of the high value of lettuce and the number of hectares devoted to its production in California, any disease or disease complex that interferes with consistent yield is a cause for grave concern.

Many diseases affect lettuce (1), some consistently causing losses and others occurring sporadically or rarely. We are limiting this discussion to the economically important diseases that have had a major impact on the lettuce industry.

Lettuce Mosaic Virus

Several viruses infect lettuce and cause diseases (1) but most are not widespread or economically important. The potentially most destructive virus disease is lettuce mosaic (9). Lettuce mosaic virus (LMV) is a typical member of the potato virus Y (potyvirus) group, with flexuous filamentous rods about 750 × 13 nm. The virus is sap-transmissible but in the field is aphid-transmitted in a nonpersistent manner. The host range is wide, including 20 genera in 10 families. LMV is seed-transmissible and thus is found wherever lettuce is grown throughout the world.

Young plants infected with LMV show a slight inward rolling along the axis of the leaf. The first true leaves of infected plants are often irregular and slightly lobed. These symptoms are accompanied or followed by light green to yellow mottling (Fig. 1A). In the young rosette stage of growth, infected plants may show veinclearing and bronzing. Mottling symptoms usually are indistinct in older plants. Half-grown to mature plants are severely stunted and dull green to light yellow (Fig. 1B). The tips of the outer leaves roll downward, and the plant appears wilted. Any mottling distinguishable at this time is best seen near the leaf margins.

Although lettuce mosaic was recognized in young plants, the different appearance of the syndrome in older plants was considered to result from an undefined disease complex called June yellows. The conclusion that LMV was the major cause of June yellows in the Salinas Valley of California resulted in a control program based on the use of virus-free seed. The state of Florida and two counties in California have adopted LMV-free seed programs. All lettuce seed to be planted in these areas must pass an assay for LMV before being distributed for sale. If one seed in 30,000 is infected with LMV, the seed lot cannot be sold or grown in the areas that have adopted the virus-free seed program. Grow-out tests and sap inoculation of *Chenopodium* indicator plants have been used as assay methods. Recently (8), an enzyme-linked immunosorbent assay (ELISA) has been developed for LMV. This sensitive procedure is faster and cheaper than the older methods and requires less space. The use of LMV-free seed has eliminated lettuce mosaic in the areas where the assay program is enforced.

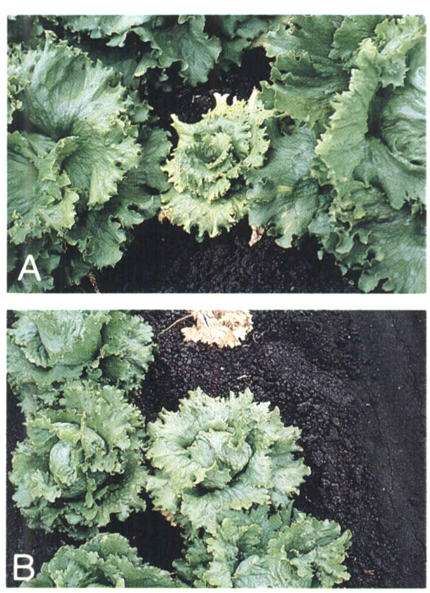


Fig. 1. Symptoms of lettuce mosaic virus infection include (A) mottling and leaf bronzing (middle plant) and (B) pale green color and downward turning of leaves (center plant).

Internal rib necrosis and rusty brown discoloration are preharvest and postharvest disorders, respectively, that occur only in the crisphead lettuce cultivar Climax (3,13). Internal rib necrosis is characterized by necrosis of parenchyma cells in the midrib. Symptoms appear as the crop matures and are especially severe in hard, overmature heads. A diffuse, dark gray-green discoloration occurs inside the lower midrib between the vascular bundles (Fig. 2). The epidermis is not affected. The wrapper and outer head leaves are most susceptible to internal rib necrosis, but occasionally symptoms develop on the inner leaves. Rusty brown discoloration is characterized by necrosis of

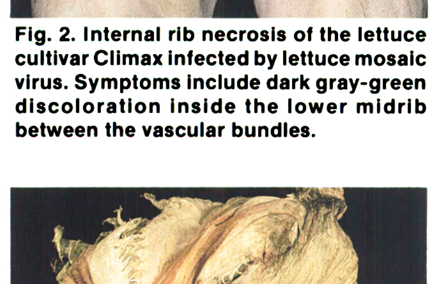


Fig. 2. Internal rib necrosis of the lettuce cultivar Climax infected by lettuce mosaic virus. Symptoms include dark gray-green discoloration inside the lower midrib between the vascular bundles.

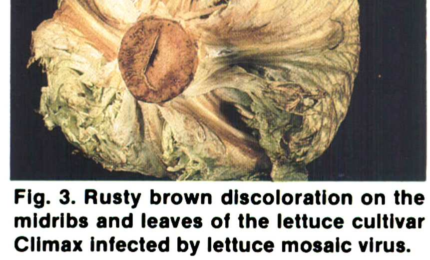


Fig. 3. Rusty brown discoloration on the midribs and leaves of the lettuce cultivar Climax infected by lettuce mosaic virus.

the epidermal cells; on severely infected heads, the midribs or entire leaves may be discolored (Fig. 3). The discoloration tends to follow—but is not confined to—the leaf veins. Sometimes the veins appear normal and the interveinal tissue is discolored.

In one study (3), Climax lettuce infected by LMV showed symptoms of internal rib necrosis during growth and symptoms of rusty brown discoloration during storage at 1 C. Virus-free Climax and LMV-infected or noninfected lettuce cultivars Calmar and Vanguard did not show symptoms of either internal rib necrosis or rusty brown discoloration. These and other results (3) confirm that LMV is responsible for the development of internal rib necrosis and rusty brown discoloration on Climax lettuce. Both disorders are genetically related to the cultivar Climax and have been controlled by the use of LMV-free seed.

Big-vein Disease

The viruslike agent causing big-vein disease is graft-transmissible but in nature is transmitted by the soilborne chytrid *Olpidium brassicae* (2). Polyacrylamide gel electrophoretic analyses detected disease-specific double-stranded ribonucleic acid in infected roots but not in infected leaves or healthy tissue (14). Conventional methods have not detected virus particles in infected lettuce tissue, and the nature of the big-vein agent is still unknown.

O. brassicae infects lettuce seedlings in field soil as early as 8 days after planting during the summer and 15 days during the winter (2). Big-vein symptoms appear about 6 weeks after planting. Leaves of infected plants assume an upright appearance, and the lamina area along the veins becomes translucent, giving the veins an enlarged appearance (Fig. 4). Stunting and delay of heading by plants in the field during cool weather have been associated with big-vein symptoms and the causative agent. These secondary symptoms, however, were absent in fumigation trials with chloropicrin or Vorlex that did not control *O. brassicae* or the big-vein agent but did control secondary organisms (2). Thus, secondary organisms probably parasitize the roots of plants infected by the big-vein agent and cause stunting and delay in heading during cool weather.

The big-vein agent is translocated to the top of plants 1–4 days before symptom expression (23); translocation is fastest at 18 and 22 C and slowest at 10 C. Translocation can occur at temperatures unfavorable for symptom expression (24 C), and the big-vein agent persists in some shoot tips at this temperature for about 1 month. Symptom expression, however, is affected by the temperature of the tops of plants. Symptoms are severe if the tops are at 14 C, whether the roots are at 14 or 24 C; no symptoms develop in infected plants if the tops are at 24 C and the roots at 14 or 24 C.

Big-vein disease can be avoided during cool, wet periods by planting in fields with no history of the disease or with light, sandy, well-drained soil. Soil fumigation with methyl bromide controlled *O. brassicae*, reduced the incidence of big-vein disease in two successive lettuce crops, and increased the rapidity and uniformity of maturity (2). Lettuce cultivars tolerant to big-vein disease are available, but horticultural characteristics vary with the area where the cultivars are grown.

Varnish Spot

Caused by *Pseudomonas cichorii*, varnish spot occurs during rainy periods or when lettuce is grown on infested soil under sprinkler irrigation. The incidence of the disease may be as high as 100%. Cool temperatures favor the occurrence of varnish spot, and the bacterium spreads in aerosols produced by splashing water. *P. cichorii* is not seedborne but is soilborne (at least for a short time) and colonizes the rhizosphere of several nonhost crops and weeds (10). The long-term survival of *P. cichorii* in soil has not been determined.

Susceptibility of lettuce to *P. cichorii* and the occurrence of varnish spot are influenced by the physiological age of the plant. Lettuce seems to be susceptible only at or near maturity. The unique symptom of varnish spot is brown discoloration of the inner cap leaves (Fig. 5). The lesions remain firm and do not decay, as does lettuce tissue infected by soft rot bacteria. Lettuce heads infected by *P. cichorii* are nonmarketable. Because the symptoms are visible only when the head is cut open, the grower is forced to abandon the harvest even in fields with only a few infected heads.

Efficient control procedures have not been developed. Copper fungicide sprays have been tested but do not control varnish spot completely. In semiarid and arid lettuce-growing areas, varnish spot can be controlled by planting during dry periods and using furrow instead of sprinkler irrigation. No lettuce cultivars resistant to *P. cichorii* are available.

Fig. 4. Lettuce infected by the big-vein agent has upright appearance and translucent veins.

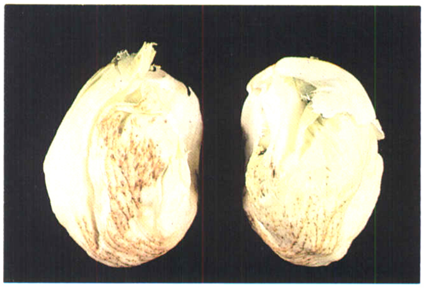


Fig. 5. Varnish spot of lettuce, showing brown discoloration of the inner cap leaves. Unlike tissue infected by soft-rot organisms, the tissue does not soften.

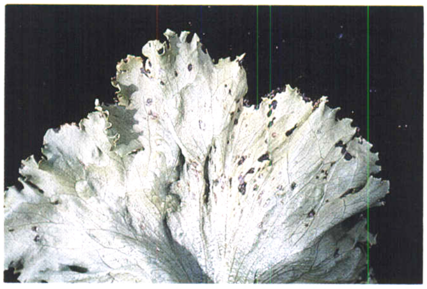


Fig. 6. Numerous dark lesions of bacterial leaf spot and head rot (*Xanthomonas campestris* pv. *vitians*) of lettuce. (Courtesy A. S. Greathead, Monterey County Cooperative Extension, Salinas, CA)

Fig. 7. Corky root of lettuce, showing forked, corky appearance of roots and vascular discoloration and necrosis.

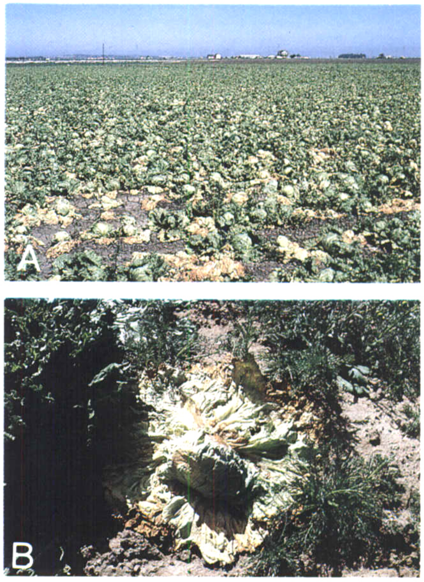


Fig. 8. Lettuce drop: (A) Severely affected field and (B) typical wilt symptom.

Bacterial Leaf Spot and Head Rot

Bacterial leaf spot and head rot, caused by *Xanthomonas campestris* pv. *vitians*, occurs during periods of rainfall or under sprinkler irrigation. *X. c.* pv. *vitians* is seedborne and favored by warm temperatures (21), so the disease is limited to the warmer lettuce-growing areas. Bacterial leaf spot and head rot has been reported in California (21), but occurrence of the disease is rare.

Bacterial leaf spot and head rot is characterized by circular or irregular, translucent, water-soaked leaf lesions that become dark brown with age (Fig. 6). The disease seldom, if ever, kills plants, but the crop may become unmarketable depending on severity of infection. The older leaves are more susceptible and may be killed, although defoliation is rare. Infection is through the stomata and hydathodes and is favored by high relative humidity, dew, or rain. The bacteria exude from the lesions and are spread in aerosols formed from windblown water droplets. Control procedures have not been defined, but theoretically, the disease could be controlled by planting indexed seed free from *X. c.* pv. *vitians* (7) in noninfested fields.

Bacterial Soft Rots

Erwinia carotovora and *Pseudomonas marginalis* are the primary causes of bacterial soft rots; *P. marginalis* is the most common cause in California. In the field, lettuce is not affected seriously by the disease except under extremely wet and rainy conditions. Soft rot bacteria are wound-invading, facultative pathogens of overmature lettuce and lettuce in transit and storage, especially at above-optimal temperatures. Thus, bacterial soft rots can be controlled by harvesting lettuce at optimal maturity, avoiding injury to the crop during harvest, and maintaining transit and storage temperatures as close to 1 C as possible.

Corky Root Rot

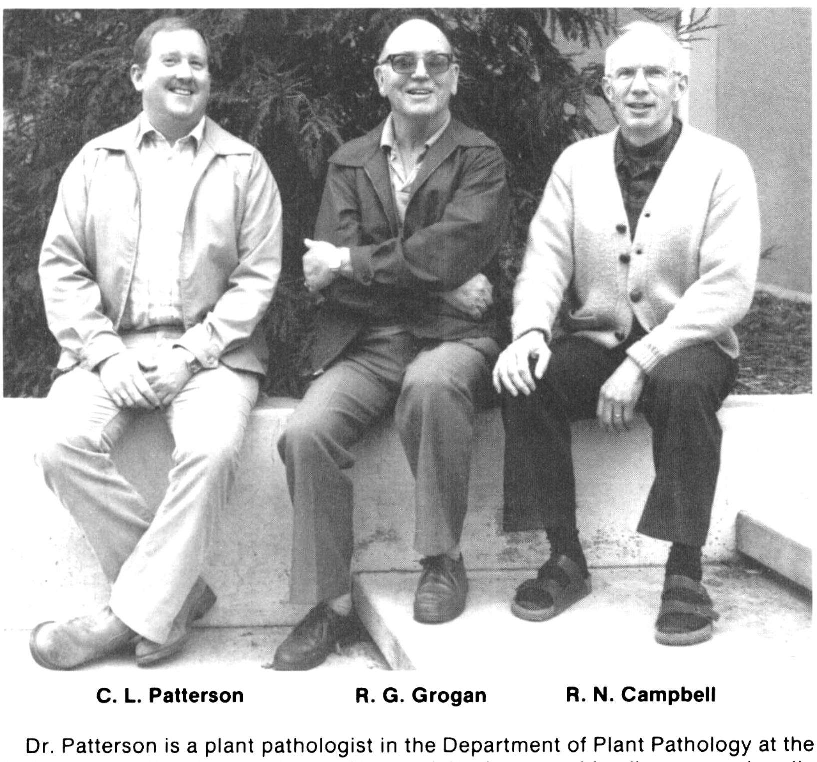
Corky root of lettuce has occurred in California, Florida, New York, and Wisconsin for several years. The disease is first evident at thinning time (four- to six-true-leaf stage) as yellow or brown-banded lesions along the taproot. In time, the lesions increase in number and coalesce, giving the roots a corky appearance (Fig. 7). The roots become brittle and break readily when bent. Other symptoms include formation of multiple taproots, xylem discoloration, and necrosis. Eventually, the secondary feeder roots turn yellow and die. Aboveground symptoms of corky root may be inconspicuous, but severely infected plants are stunted, chlorotic, wilted during the heat of the day, and not harvestable.

Although the corky root agent was transmissible by adding a small amount of infested field soil to sterile soil, the etiology of the disease was determined only recently (22). Corky root is caused by a gram-positive, non-spore-forming coryneform bacterium. The genus has not been determined.

Corky root can be controlled in the field by cultural practices that increase soil water drainage and aeration (19). These include cover cropping with a small grain (e.g., rye), deep tillage, planting lettuce on raised beds, and, with irrigation, avoiding prolonged saturation of the soil during the thinning to rosette stages of growth. Lettuce cultivars resistant to corky root are available but have horticultural characteristics not suitable for production in California. Fumigation with combinations of methyl bromide and chloropicrin provides excellent control of corky root but is too expensive to be economically practical.

Lettuce Drop

One of the most widespread and destructive diseases of lettuce is drop (Fig. 8A), named for the rapid wilting (Fig. 8B) and dying of infected plants. Drop occurs wherever lettuce is grown. The disease is caused by two species of *Sclerotinia, S. minor* and *S. sclerotiorum*. Both species have a wide host range and infect herbaceous and woody plant species in 64 families and 225 genera. The differences in the epidemiology and control of lettuce drop caused by *S. minor* and *S. sclerotiorum* have been defined (17). The important difference is the means of infection. The soilborne sclerotia of *S. minor* are small (0.5–3.0 mm) (Fig. 9A) and directly infect lettuce roots, crowns, and leaves on or near the soil surface by eruptive myceliogenic germination (a mass of hyphae emerging from the sclerotium); a senescent food base is not required for infection. The sclerotia of *S. sclerotiorum* are about 4–20 times larger than those of *S. minor* (Fig. 9B). During prolonged cool, wet periods, the sclerotia germinate by producing apothecia that forcibly discharge windblown ascospores (Fig. 10). The ascospores are ellipsoid, hyaline, and 10–14 × 4–5 μm and germinate in free water from dew, fog, rain, or sprinkler irrigation. Infection is initiated on senescent or injured tissues, usually lower leaves beginning to senesce near



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harvesttime or leaves injured mechanically or by insects.

The amount of soilborne sclerotial inoculum of *S. minor* in a field is highly correlated with the amount of drop likely to occur (6). Therefore, sanitation practices that decrease the number of soilborne sclerotia of *S. minor* also decrease the incidence of drop. The sclerotial inoculum of *S. minor* can be reduced significantly in fields by plowing (*unpublished*) or by roguing infected lettuce plants from the field (17). Plowing buries the sclerotia at depths where they cannot germinate and infect, and roguing prevents replenishment of the sclerotial inoculum in the soil. After infected lettuce plants were rogued for 3 consecutive years, sclerotia of *S. minor* were not detected by soil sampling and the incidence of lettuce drop was reduced from about 17% to less than 0.01%. One fungicide application immediately after thinning usually will partially control lettuce drop caused by *S. minor*. When the population of soilborne sclerotia and the potential disease incidence are high, however, two additional fungicide applications at 10-day intervals may be required. The fungicide should be applied in a 12- to 15-cm band over the planting surface to form a protective barrier around the upper root and crown and between the lower leaves and the soil surface. The fungicide and the amount applied vary with local registration regulations and the level of infestation of fields by soilborne sclerotia. Fumigation of soil infested by *S. minor* with metam-sodium (Vapam) has killed sclerotia and decreased the incidence of lettuce drop, but results have been inconsistent. The fumigant has been more effective in controlling drop on sandy, well-drained soils than on heavy soils with a high clay content. Some fungi and bacteria colonize and decay sclerotia in soil, and a few of these organisms show potential as biological control agents. A green manure crop increased the sclerotia in fields (5); presumably, *S. minor* grew as a saprophyte on crop debris after incorporation into the soil.

By contrast, sanitation practices that decrease soilborne sclerotial inoculum may not control *S. sclerotiorum*, which produces airborne ascospores. Ascospores from outside sources can infect lettuce in fields where sclerotia and apothecia are not detected (17), thus replenishing sclerotial inoculum. Inasmuch as lettuce plants may become contaminated by ascospores of *S. sclerotiorum* at any time during the growing period, several fungicide applications may be required for control of drop. Applications at thinning time (as described for *S. minor*) seem to prevent the apothecial stipes from emerging through the soil surface and maturing. Foliar fungicide sprays during the rosette stage of growth are required to protect senescing lower leaves from infection by ascospores from outside sources.

Low planting beds and heavy irrigation, especially the last irrigation before harvest, seem to increase the incidence of lettuce drop caused by *S. minor* and *S. sclerotiorum* (*unpublished*). Because wet soil probably favors germination of sclerotia on or near the surface, wetting the planting surface before harvest must be avoided.

Anthracnose

Several names—shot-hole, leaf perforation, ring spot, and rust—have been applied to the disease caused by *Marssonina panattoniana*. Anthracnose, however, is the currently accepted common name of the disease (1). Several wild *Lactuca* species as well as cultivated lettuce are susceptible to the fungus.

The first symptoms of anthracnose are small, tan, water-soaked spots on the lower leaves of infected plants. The spots enlarge to about 2 mm in diameter and become straw-colored. Eventually the center of the lesion falls out, forming the characteristic shot-hole (Fig. 11). Numerous water-soaked areas on the underside of the midrib elongate, darken, and become sunken, but the tissue does not fall out. Heavy infection by *M. panattoniana* can result in poor head formation and require excessive trimming during harvest.

Free water from rain, dew, or sprinkler irrigation is required for conidiogenesis, spore germination, and infection by *M. panattoniana* (4). Infection occurs directly through the leaf epidermis or open stomata after 2–4 hours of leaf wetness. Splashing water from rain or sprinkler irrigation is the most important means of spore dissemination in the field. The distance that conidia travel depends on wind velocity but is usually short. Conidia also can be spread by cultivation when plants are wet.

Although *M. panattoniana* was thought to be soilborne (4), the

Fig. 9. Sclerotia of (A) *Sclerotinia minor* and (B) *S. sclerotiorum*.

occurrence and type of soilborne inoculum produced by the fungus was identified only recently (18). Microsclerotia (60–100 μm) form in the cells of infected lettuce tissue and are deposited in the soil when the lesion falls out to form the shot-hole. Recently, microsclerotia formed in vitro were added to sterile soil that was planted to lettuce and subjected to naturally occurring rainfall. After about 10 cm of rainfall, the plants were infected by *M. panattoniana* (*unpublished*). No anthracnose symptoms were evident on plants in noninfested soil. These results support the conclusion that the primary inoculum of *M. panattoniana* is soilborne microsclerotia. The microsclerotia have been observed germinating by producing hyphae and/or conidiophores and conidia. Inoculation of lettuce leaves with the microsclerotia resulted in infection and anthracnose symptoms. The precise mechanism of primary infection of lettuce plants by *M. panattoniana* in the field, however, has not been determined. Possibly, the microsclerotia are deposited on lettuce leaves by splashing water and infect directly, or microsclerotia on the soil surface germinate by producing conidiophores and conidia as primary infective propagules.

Anthracnose can be controlled in semiarid or arid lettuce-growing areas by planting lettuce during dry periods and avoiding sprinkler irrigation. Several fungicides are effective against *M. panattoniana* but most are protectants. Inasmuch as the conidia of *M. panattoniana* are released from leaf lesions in aerosols during rainfall or sprinkler irrigation, fungicides should be applied before rain. Application of fungicides on a weekly schedule did not control anthracnose significantly more than applications before rainfall (*unpublished*). Because the primary inoculum of *M. panattoniana* is soilborne, such sanitation practices as plowing under inoculum may decrease the initial number of disease foci in a field. Other possible control procedures include treatment of soil with fumigants and soil-applied fungicides that eliminate or prevent infection of lettuce by the primary inoculum of *M. panattoniana*. The wild species *L. saligna* is resistant to anthracnose, but the resistance has not been incorporated into cultivated lettuce.

Downy Mildew

Downy mildew, caused by *Bremia lactucae*, occurs to some extent in most areas where lettuce is grown and can cause considerable damage to lettuce planted during periods of prolonged wetness from rain, dew, fog, or sprinkler irrigation. Severely infected plants may require excessive trimming during packing, which increases production costs. Invasion of downy mildew lesions by secondary soft rot organisms is another major source of crop loss in the field or in transit and storage (11).

The first symptoms are pale green to yellow spots on the upper side of the infected leaf. These circular lesions may coalesce to affect large interveinal areas and become angular in appearance. Sporulation usually occurs on the underside of the leaf (Fig. 12) but can occur on both leaf surfaces, primarily in the young seedling stage before or at thinning (11).

Soilborne oospores are the likely source of primary inoculum of downy mildew. The sporangia, however, are the means by which the fungus is disseminated. These spores serve in short-term survival of *B. lactucae* in areas of continuous and overlapping lettuce crops (11) and on *Lactuca* species weed hosts. Sporangial production is greatest in the presence of free water when the air temperature is 10–16 C (20). Sporangia are relatively short-lived but are windblown and can be carried long distances, depending on wind speed, relative humidity, amount of direct sun, and temperature. Climatic conditions that favor sporulation are also optimal for sporangial germination. Germination of sporangia to produce motile zoospores is rare; germination usually occurs by production of germ tubes. The lettuce hosts are infected directly through the leaf epidermis or open stomata.

Downy mildew has been successfully controlled by the use of resistant lettuce cultivars. Because at least 11, and possibly 13, pathogenic races of *B. lactucae* exist, duration and longevity of resistance vary with the presence, number, and aggressiveness of the races occurring in any lettuce production area. Most of the several fungicides effective against downy mildew are protectants. The systemic compound metalaxyl is curative, but because repeated use has resulted in resistant strains of *B. lactucae*,

Fig. 12. Sporulation on underside of lettuce leaf by *Bremia lactucae*, cause of downy mildew.

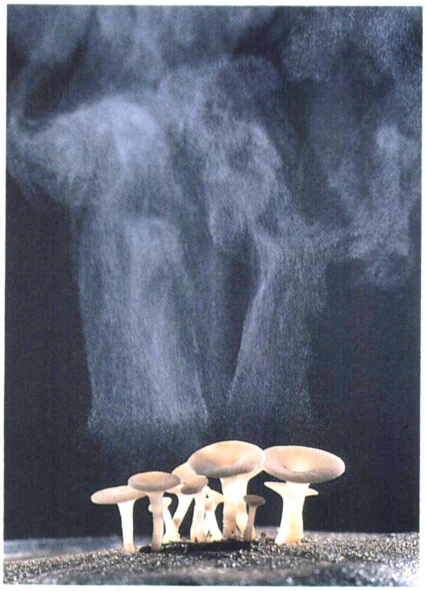

Fig. 10. Ascospore discharge by apothecia of *Sclerotinia sclerotiorum*. (Courtesy J. Clark, IPM Manuals, University of California, Davis)

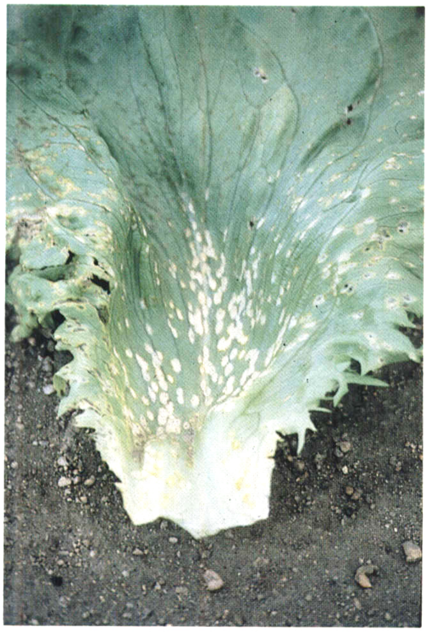

Fig. 11. Straw-colored lesions and shot-hole symptoms of anthracnose.

Fig. 13. The "string-of-pearls" symptom of the lettuce root-knot nematode *Meloidogyne hapla*. (Courtesy A. S. Greathead, Monterey County Cooperative Extension, Salinas, CA)

combining or alternating metalaxyl with other fungicides is recommended.

Root-knot Nematode

Of the approximately seven nematode species that parasitize lettuce (1), root-knot (*Meloidogyne* spp.) is the most important (12). Root-knot nematode is favored by warm temperatures and therefore usually is not a problem on lettuce, a cool-weather crop. Foliar signs sometimes are not distinctive, but symptoms of root-knot nematode are readily recognized by examining infected roots. The male and female nematodes feed on and invade the fine, newly formed lettuce roots. The female remains within the roots to produce large swellings or galls resembling a string of loosely strung pearls (Fig. 13).

A number of chemicals, particularly soil fumigants, are effective against root-knot nematode. Such nematicide fumigants as D-D, dichloropropene (Telone), and chloropicrin show good results when applied in accordance with the labels. Nematodes migrate in soil during dry periods, however, and some may escape fumigation. Therefore, soil tilth and moisture content must be considered when fumigants are applied. Further, some soil fumigants for nematode control are being banned in several agricultural areas. If this trend continues, losses caused by root-knot nematode may increase.

Fig. 14. Tipburn of lettuce, an abiotic disease related to cultivar susceptibility, temperature, and available calcium. (Courtesy I. J. Misaghi, University of Arizona, Tucson)

Fig. 15. Characteristic symptoms of russet spotting, an abiotic disease of lettuce occurring during transit and storage, are tan, reddish brown, or olive sunken lesions on the midrib and leaf tissue. (Courtesy L. J. Morris, University of California, Davis)

Tipburn

Tipburn, the most important in-field abiotic disease of lettuce, occurs during periods of high daytime temperatures (>30 C) at or near harvest (15). At high temperatures, growth rate, respiration, and organic acid production by the lettuce plant increase (16). Presumably, the organic acids sequester calcium that would normally be more available for the rapidly growing internal lettuce tissue. The first symptoms of tipburn are visible after head formation as small, dark brown spots about 0.5 cm from the edge of the young inner cap leaves. The affected areas enlarge to encompass the leaf margin, and damage may be severe (Fig. 14). Because external symptoms of tipburn usually do not occur, lettuce growers are forced to abandon fields even when only a few heads are affected.

Attempts to control tipburn by soil or foliar applications of $CaCl_2$ have not succeeded, and neither has acidification of soil to release insoluble calcium ($CaCO_3$ and $CaSO_4$). Tipburn has been controlled, however, by planting tolerant lettuce cultivars during periods when the air temperature is likely to be conducive to the occurrence of the disorder.

Russet Spotting

An important abiotic disease of lettuce that can result in considerable economic losses is russet spotting (13), caused by accumulation of ethylene gas in transit and storage containers. Russet spotting may occur anywhere in the head except the heart leaves. The small tan, reddish brown, or olive spots (Fig. 15) are mostly on the midrib but may develop on other parts of the leaf. The spots are pitlike on the midrib and shallow, rounded, and diffuse on the blade. The lesions usually involve only the epidermal cells but some extend through the leaf. Russet spotting can be controlled by preventing exposure of lettuce to ethylene during transit and storage, achieved by harvesting lettuce at optimal maturity, keeping transit and storage temperatures near 1 C, and not storing lettuce with other vegetables or fruit that liberate ethylene gas.

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