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Progress Toward Integrated Management of Lettuce Drop

Cultivated lettuce (*Lactuca sativa*) is thought to have originated around the Mediterranean from wild lettuce, *L. serriola,* commonly referred to as the prickly lettuce. The resemblance of wild lettuce to its probable wild progenitor (*L. serriola*) supports this hypothesis. The earliest written records of Herodotus indicate lettuce cultivation dating back to 550 B.C., although its appearance in stylized paintings in 4,500-year-old Egyptian tombs indicates a much more ancient history. Lettuce was brought into the New World by Christopher Columbus (54). Early in the settlement of North America by Europeans, lettuce was important and grown in market gardens near cities primarily for local consumption, as well as in home gardens. The development of the western shipping industry during the early part of this century transformed lettuce into an economically viable commodity (54).

Types of lettuce. Since its domestication as a vegetable crop, a medley of lettuce types has been described. The cultivation of specific types of lettuce is dictated by a combination of geography, climate, consumer preference, and market forces. The common types of lettuce grown throughout the world are crisphead, romaine, green or red leaf, butterhead, Batavia, Latin, stem, and oilseed types. Crisphead lettuce is also commonly referred to as "iceberg," the name of an old cultivar and technically an incorrect designation for crisphead lettuce. The four principal types of lettuce that predominate commercial production in the United States are crisphead (the most widely grown), romaine, green or red leaf, and butterhead (Fig. 1). The characteristics that distinguish these four types are the formation of a head, its shape and size, and texture (54). Lettuce is rich in vitamins A and C, and minerals such as calcium, potassium, and sodium. Crisphead lettuce has by far the least amount of vitamins and minerals, followed by increasingly higher amounts in butterhead, leaf, and romaine types (54). The generalized growth stages of a crisphead lettuce are depicted in Figure 2.

Lettuce production. Major lettuce producing countries of the world include Belgium, France, Germany, Great Britain, Italy, the Netherlands, Spain, and the United States. Lettuce production also occurs to a lesser extent in Australia, Japan, Israel, and Taiwan (55). The United States is the largest producer of lettuce, with an aggregate production area of 108,000 ha and a farmgate value of more than $1 billion annually (Table 1). Crisphead lettuce accounts for 75% of the production area and 80% of the crop value. The remaining production in the United States is comprised of leaf, butterhead, and romaine types.

In the United States, commercial production of all lettuce types is concentrated in California and Arizona. California produces more lettuce than any other country in the world, and Arizona produces more than most other countries. Annually, lettuce production in these two states alone accounts for nearly 90% of the total U.S. production, with California contributing approximately 75% of the total (Table 1). The remaining 10% of U.S. lettuce is grown in Colorado, Florida, Michigan, New Mexico, New York, New Jersey, and Ohio (54).

In California, major lettuce production is concentrated in the coastal areas of the Salinas and Santa Maria valleys. Although lettuce production can occur year-round in both valleys, in Salinas it is interrupted by the "lettuce-free" period between 7 and 21 December mandated by Monterey County as a means of avoiding lettuce mosaic in succeeding lettuce crops. Significant production occurs during late fall and winter in the San Joaquin, Imperial, and Palo Verde valleys in California. Most of the Arizona production occurs during the late fall and winter (54) and is concentrated in the western part of the state.

Three diseases that result in significant economic losses worldwide and in California are downy mildew (*Bremia lactucae*), corky root (*Rhizomonas suberifaciens*), and lettuce drop. In this paper, only lettuce drop, caused by *Sclerotinia sclerotiorum* and *S. minor,* will be discussed.

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Table 1. Major lettuce producing countries of the world[x]

Country State	Production area (ha)	Production (t)	Value ($) (×1000)
Australia	4,000	99,000	43,000
Belgium	2,400	87,600	…[y]
France	13,400	344,500	…
Germany	4,900	118,800	…
Israel	1,450	90,000	34,800
Italy	58,000	…	…
Japan	23,000	520,000	1,500,000
The Netherlands	1,000	…	63,000
Spain	34,000	968,000	…
United Kingdom	6,900	201,000	73,000
United States[z]	105,000	3,800,000	1,100,000
Arizona	24,000	900,000	180,000
California	72,500	2,800,000	872,000

[x] From reference 55.
[y] Data not available.
[z] Lettuce-prodcing states include Colorado, Florida, Michigan, New Jersey, New Mexico, New York, and Texas. Arizona and California are presented separately.

Lettuce Drop

The disease was termed Sclerotiniose when it was first discovered, but drop is the most common name used today. In the United States, Stevens and Hall (57) reported the appearance of the disease in 1890 on greenhouse-grown lettuce in Massachusetts. The occurrence of drop in Florida was reported in 1896 and from North Carolina in 1897. The appearance of drop was later documented from Pennsylvania, Kentucky, and Arizona (53). Although the symptoms described in some of these earlier reports matched the symptoms caused by *Sclerotinia,* they were attributed to pathogens such as *Botrytis* sp., *Sclerotium rolfsii,* and *Rhizoctonia* sp. The definitive corroboration of *Sclerotinia* spp. as the cause of lettuce drop was provided by Smith (56) in 1900.

Lettuce drop has been reported from all lettuce-growing regions of the world (11,22,27,34,42,50). In the United States, lettuce drop occurs in all major lettuce-producing states, including Arizona, California, Florida, New Jersey, and New York. It is common to find some symptomatic plants in most production areas. Precise statistics for annual losses caused by let-

tuce drop are not available, but they have varied from <1% to nearly 75% (53). Conditions such as cropping history, irrigation and tillage methods, and other environmental and cultural characteristics of the field influence losses. In California, average seasonal losses of up to 15% from lettuce drop are common, and individual fields with losses of up to 60% are not uncommon. Economic losses are increased by higher lettuce prices in some seasons.

All types of lettuce are affected by *Sclerotinia* spp. Because most land is in crisphead lettuce production, most of the information was developed from lettuce drop on crisphead lettuce, but this information is applicable to all types of lettuce.

Causal agents. Lettuce drop is caused by *Sclerotinia sclerotiorum* and *S. minor.* As early as 1900, Smith (56) noticed the distinction between cultures of *Sclerotinia* that produced large and small sclerotia. Subsequently, Jagger (34) observed that lettuce drop in New York was caused mostly by the undescribed species of *Sclerotinia* that produced only small sclerotia, and later described the species as *S. minor.* Both species are widely distributed wherever lettuce is grown, but only one species

or the other causes losses in most locations. Reports from Canada (44), New Zealand (27), and New York (1) indicate the disease is caused by only *S. minor,* and in most other regions except California, lettuce drop is predominantly caused by *S. sclerotiorum.* California is unique with respect to the distribution of the two species in lettuce production areas. In the Salinas Valley and adjoining coastal valleys, the predominant cause of lettuce drop is *S. minor,* while in the San Joaquin Valley, the majority of lettuce drop infections are caused by *S. sclerotiorum.* In the Santa Maria and Lompoc areas, infections are caused by either species, although the dominant species is *S. minor.* Rare infections by *S. sclerotiorum* are observed in the Salinas Valley. They originate from germinated sclerotia, whereas in the San Joaquin Valley, the majority of infections caused by this species originate from airborne ascospores. The reasons for these specific niches, and the resultant geographical isolation, are unknown.

Even though Smith (56) noticed the distinction between *Sclerotinia* producing the large and small sclerotia as early as 1900, Jagger (34) determined that the pathogen

Fig. 1. Lettuce types cultivated in the United States: (A) crisphead, (B) romaine, (C) green leaf, and (D) butterhead. Reprinted with permission from the American Phytopathological Society, St. Paul, MN.

producing smaller sclerotia was a new species. Nomenclatural problems persisted in *Sclerotinia* spp. until the late 1970s. For some time, the two pathogens were referred to as *S. sclerotiorum* (=*Whetzelinia sclerotiorum* [17]) and *S. sclerotiorum minor* in the literature (41). Because of the difficulty in delineating species based on characteristics such as the sizes of sclerotia, asci, and ascospores, Purdy (53) grouped these two species along with two other species. Others found enough distinctive characteristics in the size, shape, amount, and pattern of sclerotia formation in culture media, types of tissue lining apothecia, and number of nuclei in the ascospores to call them distinct species (35). Based on this work, the two causal agents of lettuce drop have been routinely designated *S. minor* and *S. sclerotiorum*.

The distinctive features of *S. minor* include mostly circular (0.5 to 2.0 mm diameter) sclerotia (Fig. 3A) and tetranucleate ascospores. In addition, carpogenic germination and production of apothecia are extremely rare because sclerotia germinate eruptively. In contrast, sclerotia of *S. sclerotiorum* measure 2 to 20 × 3 to 7 mm and are irregularly shaped (Fig. 3A). Each sclerotium germinates carpogenically, producing one to several apothecia that are usually cup-shaped but sometimes are ex-

panded and flat with a central dimple (35). Apothecia are usually white, yellow, or a shade of brown (Fig. 3B). Asci are cylindric-clavate, measuring up to 130 × 10 mm, and contain eight binucleate ascospores. The ascospores are nonseptate, uniseriate, hyaline, and elliptical (9 to 13 × 4 to 5 mm). Application of restriction fragment length polymorphisms in nuclear and mitochondrial DNA has essentially confirmed that the two species of *Sclerotinia* are distinct (35).

Host range. Host specificity is not present in either species of *Sclerotinia*. *S. sclerotiorum* has an unusually broad host range, infecting a wide range of host plants, including many economically important crop species. *S. minor* infects fewer hosts than *S. sclerotiorum* but has a wider host range than most plant pathogens (15,45).

The most recent host index (15) indicates that *S. sclerotiorum* is pathogenic to 408 plant species in 278 genera representing 78 families. A majority of these are herbaceous, dicotyledonous plant species, but several monocotyledonous and gymnosperm species are also infected by *S. sclerotiorum*. In addition, it infects one Pteridophyte species (15). In contrast, *S. minor* occurs on 94 plant species in 66 genera representing 21 families. *S. minor* is known

to infect only Angiosperms. It infects only two monocots (45). Within the Asteraceae, to which lettuce belongs, *S. minor* infects 21 species and *S. sclerotiorum* 106 species (15,45).

Symptoms. The common name of the disease on lettuce typifies the final symptoms observed on infected plants. Within a mostly healthy field, one may find infected plants that have collapsed entirely in less than 2 days—hence the name drop. Lettuce drop occurs in two phases. The first phase occurs at the rosette stage (Figs. 2 and 4A, B, and C) or immediately after thinning (3 to 4 weeks after seedling emergence) on a very low percentage of plants. The second economically significant phase occurs at or near crop maturity (Figs. 2 and 5A and B). The initial symptom is a stressed appearance due to wilting of the outermost leaves.

Infections from soilborne sclerotia and airborne ascospores are different. As infection from soilborne sclerotia progresses toward other leaf layers, the entire plant, including the head, wilts. Layers of collapsed leaves lay flat on the soil surface, giving the plant a yellowish color. Similar symptoms could result from heavy infestation by lettuce-root aphids, but the usual soft watery decay that follows on both above- and belowground plant parts is unique to lettuce drop. Subsequently, under
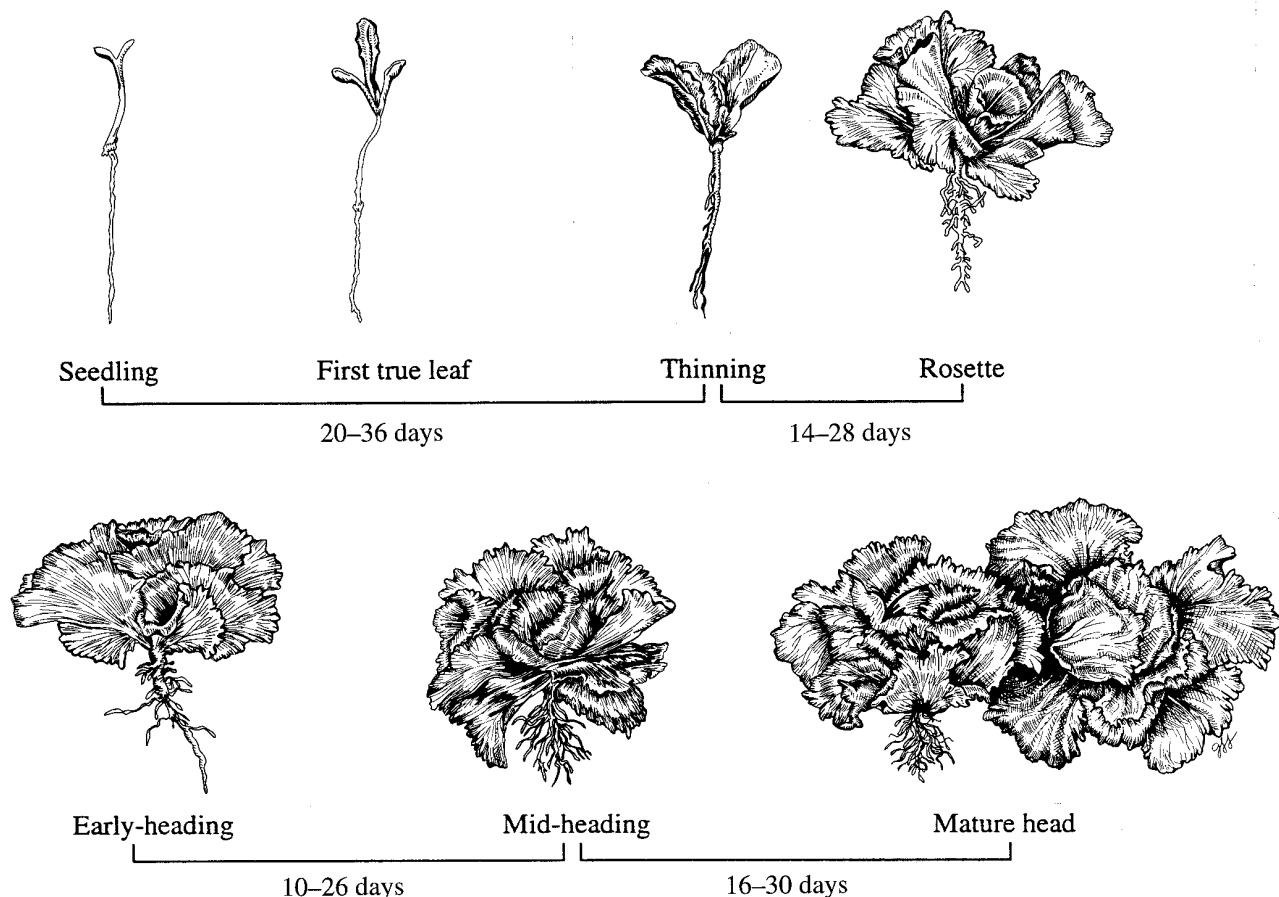

Seedling First true leaf Thinning Rosette

20–36 days 14–28 days

Early-heading Mid-heading Mature head

10–26 days 16–30 days

Fig. 2. Typical growth stages of crisphead lettuce. Reprinted with permission from the American Phytopathological Society, St. Paul, MN.

moist conditions, the fungus produces a snowy white mycelium on infected plant parts (Fig. 6A). Black sclerotia are produced on the lower surface of the leaves touching the soil, around the crown, and throughout the taproot (59). Their size depends on fungal species and the temperature during their formation (13,33).

When airborne ascospores initiate infection, losses can be as high as 70%. Symptoms are similar to those described above, except they originate on exposed areas of the lettuce plant, where the ascospores settle and infect. Abundant white, cottony mycelium develops on affected tissues, subsequently producing large, irregularly shaped black sclerotia (Fig. 6B).

Pathogenesis. The pathogenesis of diseases caused by *Sclerotinia* spp. is complex, and much of the current knowledge on pathogenesis comes from studies on *S. sclerotiorum* (39). The ability of *Sclerotinia* spp. to infect and penetrate host tissue depends on the type of inoculum, the nutrient status of the fungus, and environmental conditions. De Bary observed that *Sclerotinia* requires external nutrients for successful infection (39). *S. sclerotiorum* produces a wide array of degradative, lytic enzymes, such as endo- and exopectinases, cellulases, hemicellulases, and proteases, that are believed to facilitate colonization and host cell wall degradation (39). The role of oxalic acid in the infection process is well documented (24,40,49). Even before the cause-effect relationship of germ theory was an accepted scientific concept, De Bary in 1886 observed an association between the production of oxalic acid in carrots and infection by *S. sclerotiorum* (39). Recent studies (24) with oxalic acid-deficient mutants of *S. sclerotiorum* have implicated oxalic acid as a pathogenicity determinant. While the mutants were identical to their wild-type counterparts except for the production of oxalic acid, they were unable to cause infection or to form sclerotia. Despite possessing a full complement of degradative enzymes, including polygalacturonase, pectin methylesterase, and cellulase, the mutants were all non-pathogenic, suggesting that these enzymes were important for tissue maceration but not sufficient for disease establishment

(24). Oxalic acid produced by the pathogen, upon successful entry into the host, reduces the pH of the host tissue, which decreases host cell viability and therefore its ability to respond to pathogen invasion (40). Oxalic acid may also sequester Ca^{2+} from calcium pectate of the host cell wall, favoring polygalacturonase activity (49). Additionally, calcium oxalate crystals may occlude xylem vessels, leading to wilt symptoms (49).

Recent studies (21) have ascribed yet another role for oxalic acid in pathogenesis. The reduced pH in host tissue, as a
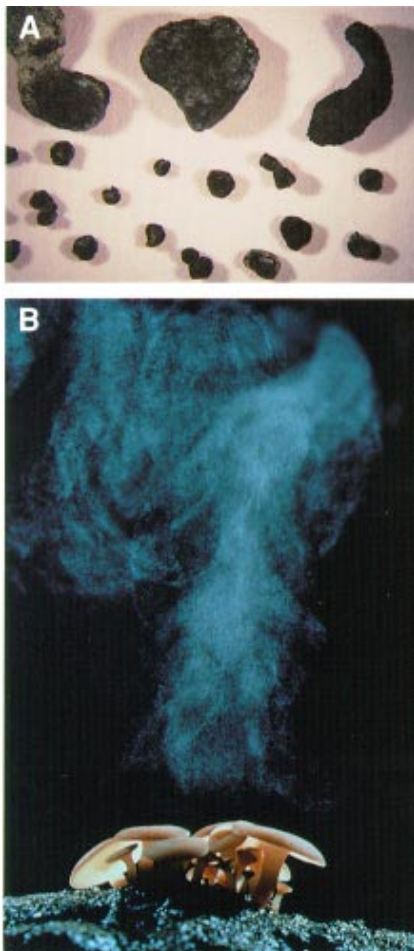
Fig. 5. (A) Plants killed by airborne *Sclerotinia sclerotiorum* ascospores. (B) Lettuce drop at crop maturity.

Fig. 3. (A) Large, irregular *S. sclerotiorum* sclerotia (top, magnified ×8) and small, mostly circular *S. minor* sclerotia (bottom, magnified ×8). (B) A carpogenically germinated sclerotium of *S. sclerotiorum* with a number of apothecia and the ascospore cloud emanating from them. Reprinted with permission from the American Phytopathological Society, St. Paul, MN.
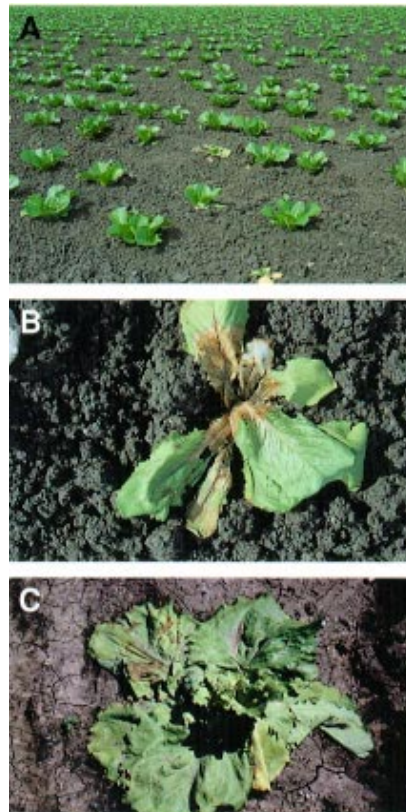
Fig. 4. (A) Lettuce drop caused by *Sclerotinia sclerotiorum* via mycelial contact at the rosette stage. (B) Water-soaked and rotted crown of an infected lettuce plant. (C) Lettuce drop caused by *S. minor* at rosette stage. Reprinted with permission from the American Phytopathological Society.
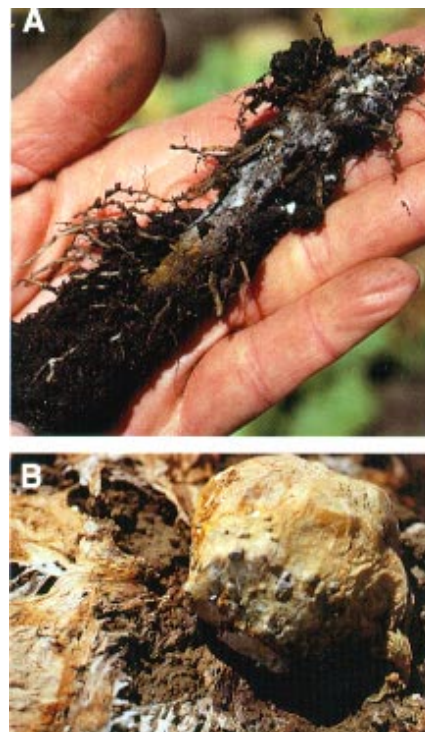
Fig. 6. (A) Extensively colonized taproot of a lettuce plant converted into sclerotia. (B) A close-up of a degenerated lettuce plant with abundant sclerotia.

result of production of oxalic acid by *S. sclerotiorum,* also inhibits enzymes, such as *o*-diphenol oxidase, that are implicated in host defense mechanisms. Thus, the inhibition of *o*-diphenol oxidase by oxalic acid distinctly enhances the pathogenicity of *S. sclerotiorum* (21).

Disease cycle and epidemiology. The characteristics that separate the two species of *Sclerotinia* also significantly impact the mode of infection of lettuce plants. The generalized disease cycles for both species are presented in Figure 7.

Both species survive in soil mainly as sclerotia for up to 8 to 10 years (4,13), but they may also survive as active mycelium in living or dead plants (16). Survival of sclerotia of both species is affected by the location of sclerotia along the soil profile, duration of burial, soil moisture, and soil temperature. The viability of sclerotia is reduced over time and with increasing soil moisture. In saturated soil, sclerotia of *S. minor* disintegrate or fail to germinate within 8 weeks (32). Thermal inactivation of *S. minor* sclerotia occurs at 40°C within 39 h, at 45°C within 6 h, and at 50°C within 2 h (4). *S. sclerotiorum* sclerotia survive well for at least 15 months at depths of up to 30 cm (3). *S. sclerotiorum* sclerotia can survive up to 7 years, even when buried, under certain conditions. Nearly 90% of *S. sclerotiorum* sclerotia in the soil are thermally inactivated at 35°C

(13). Survival of *S. minor* sclerotia is also reduced in soils with heavy infestations of the dark-winged fungus gnat (*Bradysia coprophila* Lintner). Larvae of these gnats damage sclerotia directly by feeding and indirectly by increasing the colonization of damaged sclerotia by soil mycoparasites (25).

Germination of sclerotia in both species is negatively affected by the quantitative and qualitative microfloral content in the soil (1,16,63). *S. sclerotiorum* sclerotia below the soil surface germinate carpogenically after a period of chilling (4°C) at soil moisture near saturation for 2 or more weeks by forming apothecia that produce and release millions of airborne ascospores (Fig. 3B) (20,35). Preconditioning by constant rinsing under running water enhances the production of apothecia in the laboratory (20). Greater numbers of apothecia per sclerotium are produced when the sclerotia are located in the top 5 cm of the soil profile than in deeper soil profiles (47). The formation of apothecia is strongly photo-dependent, and light intensity greater than 58.1 $\mu E \cdot s^{-1} \cdot m^{-2}$ favors the development of apothecia (35). Greater numbers of apothecia per sclerotium are produced by larger sclerotia than by smaller ones (13). Optimal temperatures of 8 to 16°C are particularly favorable for the formation of apothecial initials and ultimately apothecia. Conditions for the carpogenic germination of sclerotia of *S. minor* are rare in nature (28) and have not been quantified precisely.

Eruptive germination of *S. minor* sclerotia is affected by the moisture status of sclerotia. Sclerotia produced on the host tissues do not germinate well because of their high moisture content. They have to dry somewhat before a majority of them can germinate (51). Soil moisture and temperature significantly affect eruptive germination in *S. minor*. Germination of sclerotia occurs when soil matric potential is between –0.03 MPa and –1.5 MPa, with an optimum at –0.03 MPa (2). Germination and mycelial growth occur between 6 and 30°C, with an optimum at 18°C (33).

Infection by either species can occur at any crop growth stage, but economic losses occur most often during crop maturity. The ascospores, released over a period of 2 to 3 weeks, are dispersed throughout the lettuce field and adjacent fields by wind. After landing on senescing or dead lettuce leaves, ascospores in the presence of free water on the leaf for 48 h or more germinate to produce hyphae that infect and kill the plant by girdling the root-crown area (50). Plants infected by airborne ascospores form sclerotia on the aerial parts of the plants (Figs. 6B and 7). Mycelial infection from eruptively germinating (Fig. 8A) *S. sclerotiorum* can also occur, but infection of plants by this mode in commercial fields is uncommon (50). Because of the requirements for specific conditions to
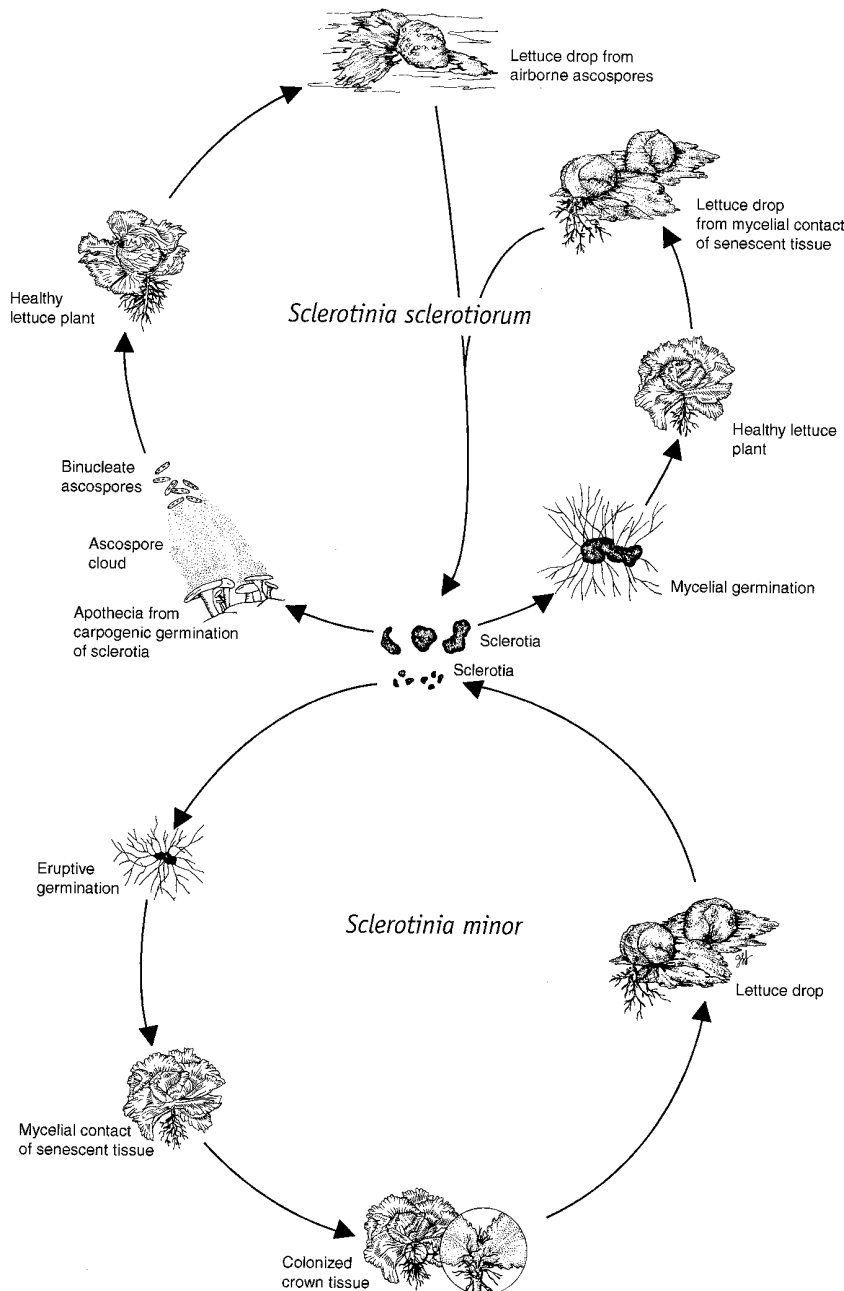

Fig. 7. Disease cycles of *Sclerotinia sclerotiorum* and *S. minor* on lettuce.

"prime" the sclerotia to produce apothecia and ascospore release, lettuce drop caused by *S. sclerotiorum* is sporadic and unpredictable.

In contrast, *S. minor* sclerotia seldom produce apothecia, and infections are caused by eruptive germination of sclerotia (Figs. 7 and 8B). Sclerotia located within 2 cm of the taproot and 8 cm of the soil surface produce masses of hyphae that infect nearby roots, stems, and senescent leaves (32) (Fig. 7). Infection of lettuce plants by *S. minor* can also occur over a wide temperature range (6 to 24°C), with an optimum at 18°C (33). Plant-to-plant spread occurs occasionally by mycelial contact. Large numbers of sclerotia are formed on the crown and subterranean parts of the infected lettuce plant (Figs. 6A and 7). The sclerotia of both species are returned to the soil when the lettuce residue is disked under after harvest.

Because only sclerotia of *S. minor* located within 2 cm of the taproot and 8 cm of the soil surface are capable of infecting lettuce plants, Grogan et. al. (26) coined the terms competence distance and competence depth to describe these two factors. The total volume of soil encompassing the maximum depth and distance from which a sclerotium can infect lettuce plants, referred to as the competence volume for *S. minor*, was determined to be 100 cm^3 (26). The concept of competence volume has significant implications for soil sampling to determine the inoculum density. Soil sampling techniques to incorporate the concept of competence volume of soilborne propagules require assaying the soil samples in their entirety. We have therefore custom-designed soil samplers to obtain cores of 100 cm^3.

Disease Management

Management of lettuce drop includes chemical, cultural, biological, and physical control methods. Currently, no single management technique provides satisfactory levels of control, so growers have integrated several methods. Differences in epidemiology of the disease caused by the two species of *Sclerotinia* (50) necessitate different methods of control. The involvement of airborne ascospores in *S. sclerotiorum* makes it more difficult to manage lettuce drop caused by this species.

Chemical control. Until the mid-1970s, only one fungicide, 2,6-dichloro-4-nitroaniline (DCNA) was registered for the control of lettuce drop. Marcum et. al. (41) determined DCNA should be applied immediately after thinning for best control of lettuce drop. Subsequent post-thinning applications do not provide satisfactory control.

Other fungicides, such as benomyl, have given mixed results. Post-thinning applications of benomyl failed to control lettuce drop caused by *S. minor* in California (41)

and New Zealand (29). However, in Israel, benomyl reduced the number of sclerotia-producing apothecia and as a result, reduced the incidence of lettuce drop caused by *S. sclerotiorum* (11). Currently, benomyl does not have a lettuce label in the United States.

The advent of cyclic imides and the registration of fungicides such as iprodione (3-(3,5-dichlorophenyl)-*N*-isopropyl-2,4- dioxoimidazolidine-1-carboxamide) and vinclozolin (*RS*)-3-(3,5-dichlorophenyl)-5-methyl-5-vinyl-1,3-oxazolidine-2,4-dione), sprayed over the bed and at the base of plants immediately after lettuce thinning, dramatically improved lettuce drop control. These were the most widely used fungicides for lettuce drop control until the late 1980s. The ability of iprodione and vinclozolin to control lettuce drop was short-lived. Growers in France reported a dramatic failure of iprodione and vinclozolin to control lettuce drop (42). The lack of control is related to rapid degradation in soils repeatedly treated with these fungicides. In a study involving 33 soils from commercial fields, 90% of iprodione applied to the soils with an extensive pretreatment history degraded within 5 days, compared with more than 90 days in previously untreated soils (64). Enhanced degradation of iprodione and vinclozolin is exacerbated by both pH and soil microbial population (64). Little degradation of either of these fungicides occurred at pH 4.3 or 5.0, and degradation at pH 5.7 was slower than at pH 6.5 in soil with or without a history of iprodione or vinclozolin usage. In soil with pH 6.5, the half-life following the first, second, and third applications was 30, 12, and 4 days for iprodione and 30, 22, and 7 days for vinclozolin. Studies in France (9) confirmed these re-

sults but also demonstrated that the enhanced degradation of iprodione and vinclozolin could be reversed by soil solarization, thus implicating the involvement of soil microbes in the degradation.

In recent years, losses from lettuce drop have been severe in California despite fungicide applications. Iprodione or vinclozolin resistance was not detected in field populations of *S. minor*, but resistance could be readily induced in vitro. The iprodione-resistant strains exhibited cross-resistance against vinclozolin and vice versa. Nearly all resistant strains became avirulent 10 months after selection in vitro. Fungicide efficacy on wild-type *S. minor* population in commercial fields indicated that fungicide resistance was not the cause of control failure in coastal California fields. Application of fungicides at a less than optimal time and enhanced degradation of fungicides in California soils may explain the recent lack of control observed in coastal California (30).

Application of metham-sodium, either by sprinklers (11) or through drip irrigation, has provided encouraging results. The efficacy of metham-sodium is affected by penetration into soil, which is affected both by the soil structure and temperature. Because the toxicity of metham-sodium to the pathogens is greatest at 35°C (12), the use of this chemical for lettuce drop control has not gained wide acceptance by lettuce growers in California and elsewhere. Currently registered fungicides provide less than satisfactory control of lettuce drop caused by either *Sclerotinia* spp. Growers are therefore integrating several alternative methods along with fungicides for satisfactory management of lettuce drop.

Deep plowing and roguing. Because survival of sclerotia decreases with time
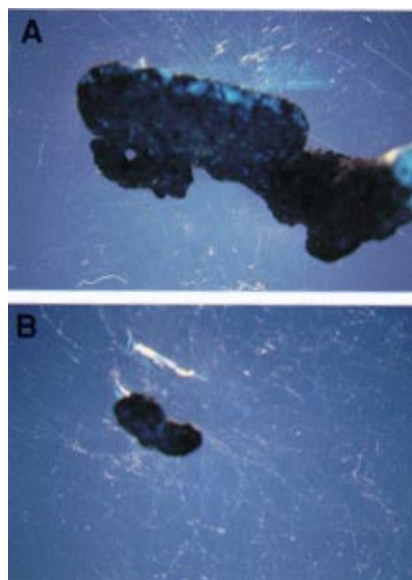

Fig. 8. (A) Eruptively germinated sclerotium of *Sclerotinia sclerotiorum*. (B) Eruptively germinated sclerotium of *S. minor*.

Fig. 9. (A) A Wilcox plow adapted for deep plowing. (B) Large clods formed as a result of deep plowing in a commercial field.

and depth of burial, movement of sclerotia to depths greater than 10 cm will prevent lettuce drop infections (26,32). Factors such as soil temperature, O_2, CO_2, and ethylene concentrations change with soil depth and may influence survival. However, Imolehin and Grogan (31) concluded that these factors are usually not limiting to the survival of *S. minor* sclerotia. The increased mortality of sclerotia at greater depths occurred because of the colonization of sclerotia by antagonistic fungi. These findings led to the development of deep plowing as a disease management practice to bury sclerotia located in the upper soil profile. Because *S. sclerotiorum* also has an airborne phase, deep plowing was not expected to be as successful as with *S. minor*. A moldboard plow was specifically designed for deep plowing (Fig. 9A), and the growers immediately adopted this technique in 1985. The initial euphoria soon gave way to disappointment as growers in the Salinas Valley in California with high inoculum densities observed that the level of lettuce drop control from deep plowing did not justify its cost.

Disease incidence was often greater in the second crop after deep plowing than prior to deep plowing. The spatial distribution of sclerotia changed from a highly aggregated pattern prior to deep plowing to a more uniform pattern. While the desired effect of reducing the number of sclerotia was accomplished with deep plowing, the altered distribution of sclerotia increased the probability of lettuce plant infection. In the Salinas Valley, two crops of lettuce are commonly grown each year in a given field, and lettuce drop infections from these crops continually add sclerotia to the soil. These sclerotia are deposited at various depths during land preparation for the next crop. In these fields, viable sclerotia are probably always present in the soil profile. Their distribution may be horizontally aggregated because many sclerotia formed on infected plants are concentrated in the area containing the debris from infected plants. Increased numbers of very large clods form as a result of soil inversion by deep plowing (Fig. 9B). Breaking these clods to prepare soil for lettuce production requires additional tillage operations. These additional tillage operations redistribute sclerotia to areas that previously lacked them and result in a greater lettuce drop incidence (62).

Because infected plants serve as the principal source of soil inoculum, roguing of infected plants over time should significantly deplete the soil inoculum reservoir. Patterson and Grogan (50) tested this hypothesis in commercial fields and observed significant reductions in the soil inoculum compared with areas where the infected plants were not rogued. Because of the labor-intensive nature of this procedure and the significant increase in the cost of lettuce production, growers have not adopted this practice.

Crop rotation and cover crops. In recent decades, the availability and cost-effectiveness of chemical fertilizers, pesticides, and soil fumigants have reduced the

Fig. 10. (A) Broccoli being chopped by a Marvin incorporator. (B) Residue on top of the planting beds immediately after chopping. (C) Low incidence of lettuce drop following incorporation of previous broccoli crop residue. (D) Severe incidence of lettuce drop under continuous lettuce production.
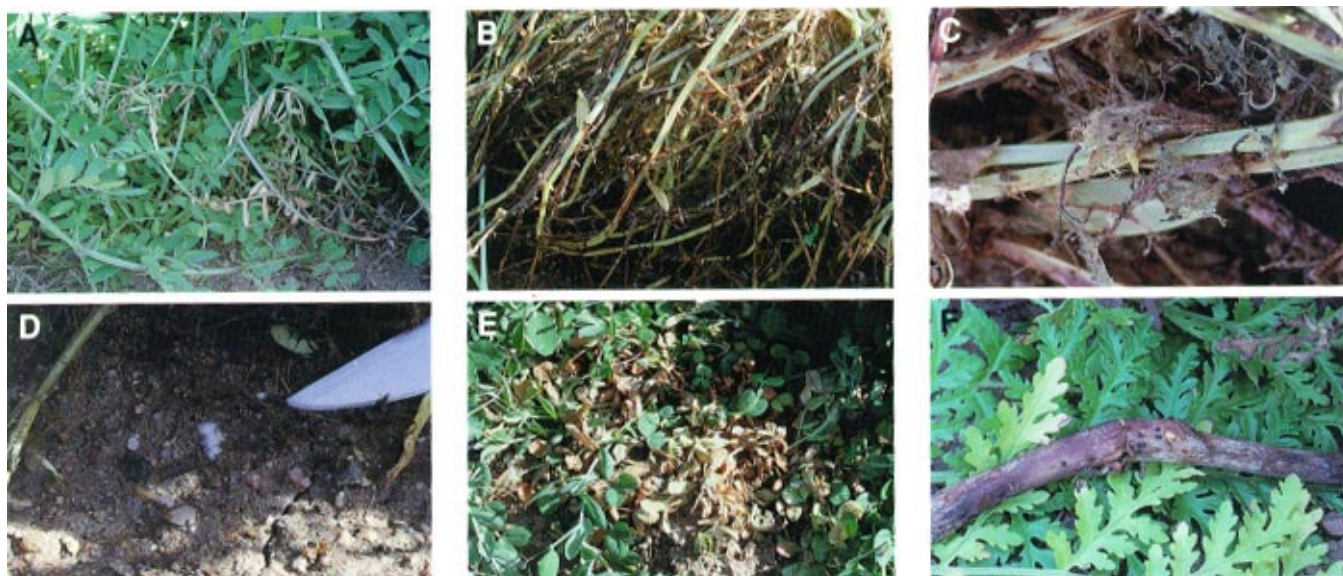

Fig. 11. (A) Early symptoms of *Sclerotinia minor* colonization of *Vicia benghalensis* stems. (B) Heavy infection of *V. benghalensis* by *S. minor* and the resultant defoliation. (C) *S. minor* sclerotia on colonized *V. benghalensis* stems. (D) Eruptive germination of sclerotia in a plot cover-cropped with *V. benghalensis*. (E) *Pisum sativum* subsp. *arvense* infected by *Sclerotinia minor*. (F) Sclerotia on infected stems of *Phacelia tanacetifolia*.

use of rotation as an agronomic tool. Pathogens such as *S. minor* and *S. sclerotiorum* are not easily managed by crop rotations because of their wide host range. Recently, however, broccoli (*Brassica oleracea* L. var. *botrytis* L.) reduced the number of *Verticillium dahliae* microsclerotia in soil and Verticillium wilt on cauliflower (60). Because *S. minor* also produces sclerotia, we evaluated rotations of lettuce with broccoli to reduce *S. minor* sclerotia and lettuce drop incidence. The 2-year sequence of treatments in this experiment included: (i) lettuce-lettuce-lettuce-lettuce; (ii) broccoli-lettuce-broccoli-lettuce; (iii) broccoli-broccoli-lettuce-lettuce; and (iv) fallow-lettuce-fallow-lettuce. To ensure the uniform availability of inoculum, all lettuce plants were individually inoculated with a mixture of mycelium-infested rye seed and *S. minor* sclerotia when the experiment was initiated in the spring of 1996. Infection of lettuce and broccoli by *S. minor* was recorded weekly. The pathogen failed to infect broccoli. At maturity, crops in the corresponding plots were chopped using a Marvin incorporator (Fig. 10A and B), and after 2 days, the residue was incorporated to a depth of 15 to 20 cm with the same equipment. One month after residue incorporation, the plots were tilled and beds were shaped for planting the next crop in each treatment. After completing the entire cropping sequence, we observed that, not only were the numbers of sclerotia in soil reduced after the broccoli residue was incorporated each season, but also the incidence of drop on the subsequent lettuce crops was significantly lower where lettuce followed broccoli than with continuous lettuce (Fig. 10C and D) or fallow followed by lettuce treatments (K. V. Subbarao, J. C. Hubbard, S. T. Koike, K. F. Schulbach, *unpublished data*). Based on the results of this study, a number of growers have already tested rotations of lettuce with broccoli and have obtained similar results. For the first time,

crop rotation could become a viable option to manage lettuce drop.

Because soil organic matter is important to soil fertility and productivity, increasing numbers of growers in the Salinas Valley have expressed interest in planting winter cover crops or green manure crops to alleviate decreased soil organic matter, poor soil fertility, poor soil structure, and nitrate loss from leaching (37,38). Among the cover crops being tested, Phacelia (*Phacelia tanacetifolia* Benth.), purple vetch (*Vicia benghalensis* L.), Lana woollypod vetch (*V. dasycarpa* Ten.), and Austrian winter pea (*Pisum sativum* L. subsp. *arvense*) are also hosts of *S. minor* (Fig. 11A to F) (19,37). Lettuce crops following these cover crops have significantly higher levels of lettuce drop compared with plots that were left fallow during the winter (19,37). The risk of increased lettuce drop in fields previously planted to the above cover crops serves as a deterrent to their adaptation by growers.

Biocontrol. Currently, no efficacious biocontrol for either species of *Sclerotinia* is available for commercial application. A number of biocontrol agents, including *Coniothyrium minitans, Gliocladium virens, Sporidesmium sclerotivorum, Talaromyces flavus,* and *Trichoderma harzianum,* have been tested. The best characterized biocontrol agents are *Sporidesmium sclerotivorum* on *S. minor* (5–8), and *C. minitans* on *S. sclerotiorum* (22,43). *Sporidesmium sclerotivorum* is widely distributed in agricultural soils of the United States and is an obligate parasite of sclerotial fungi, including *S. minor* and *S. sclerotiorum.* In extensive field tests in Beltsville, Maryland, the *Sporidesmium sclerotivorum* significantly reduced inoculum density of *S. minor,* but lettuce drop control was modest at best (6). The ability of *Sporidesmium sclerotivorum* to control *S. minor* in all soil types is questionable. Efficacy of *Sporidesmium sclerotivorum* in California lettuce fields has been disap-

pointing (36; S. T. Koike, *personal communication*). One reason for control failure is the neutral to alkaline pH of California lettuce fields. Growers in coastal California generally lime fields to avoid clubroot on cruciferous crops, which increases the soil pH to 7.0 or above. The optimum pH range for the growth of *Sporidesmium sclerotivorum* is 4.5 to 5.5 (5). Failure to control lettuce drop in acidic soils is not well understood. Biocontrol for lettuce drop is also incompatible with chemical control because of the detrimental effects of fungicides on the biocontrol agent (8). In addition to soil conditions in California that are unsuitable for maximum efficacy, the cost of using *Sporidesmium sclerotivorum* (6) discourages its use.

Much of the information on *C. minitans* has come from studies on *S. sclerotiorum* infecting canola (*Brassica rapa* L.) and sunflower (*Helianthus annuus* L.). Although the ability of *C. minitans* to reduce the viability of *S. sclerotiorum* sclerotia and apothecial production in vitro is well documented (22,43), the biocontrol agent failed to reduce disease on canola in the field. Factors affecting efficacy in the field need to be studied before biocontrol for diseases caused by *Sclerotinia* spp. is realized. Recently, using hypovirulent strains of *S. minor* for biocontrol has been suggested (14,44), but the practicality of this approach remains to be demonstrated.

Irrigation methods. Lettuce production in coastal California occurs under different types of irrigation. Traditionally, furrow irrigation was used because of the ease of operation, but water use is high and inefficient, and salt accumulation is a major problem. In the late 1960s, growers adopted sprinkler irrigation for optimal seedling emergence and plant stand establishment (10). Sprinklers offered many advantages for lettuce production, such as decreased salt accumulation near seed rows, rapid and uniform application of water, higher and more uniform seed

Table 2. Lettuce drop incidence at harvest, number of marketable heads, and total yield on two lettuce cultivars in subsurface drip- and furrow-irrigated plots during 1993 to 1995 in the Salinas Valley, CA[v]

Year and season	Cultivar	Irrigation	Drop[w] (%)	NMH[x]	Yield (kg)[y]
1993 spring[z]	Salinas	Drip	21.6 b	28.8 a	15.7 a
		Furrow	41.8 a	21.2 b	9.5 b
1993 fall	Misty Day	Drip	31.4 b	22.3 a	10.1 a
		Furrow	59.8 a	13.6 b	6.7 b
1994 spring	Salinas	Drip	3.3 b	38.3 a	21.9 a
		Furrow	33.8 a	24.3 b	14.1 b
1995 spring	Salinas	Drip	10.3 b	42.3 a	31.0 a
		Furrow	27.4 a	37.8 b	25.0 b
1995 fall	Misty Day	Drip	15.1 b	19.0 a	9.4 a
		Furrow	41.8 a	8.7 b	4.1 b

[v] Modified and reprinted with permission from reference 61.
[w] Mean lettuce drop incidence in the central 24 m^2 area on the middle four beds of each treatment plot.
[x] Mean number of marketable lettuce heads in the central 24 m^2 area on the middle four beds of each treatment plot.
[y] Mean weight of the total marketable heads.
[z] Within each column and season, the numbers followed by the same letter are not significantly ($P > 0.05$) different according to the LSD test.

emergence, more efficient use of water, and higher yields. With the potential shortage of available water for vegetable production, and the need for preventing contamination of groundwater by fertilizers and pesticides, a large number of growers are adopting subsurface drip irrigation. Subsurface drip irrigation requires about half the water needed by furrow and sprinkler systems and, since fertilizers can be applied directly to the root zone, fertilizer efficiency is increased while NO_3^- leaching is decreased. Initial installation of subsurface drip irrigation is expensive, but once the system is in place, operating costs are low.

A comparative study of furrow and subsurface drip irrigation on diseases and yield of lettuce revealed a significant reduction in the incidence of lettuce drop (Fig. 12A and B) and increased yield under subsurface drip irrigation (61; Table 2). The control achieved through drip irrigation was superior to furrow irrigation plus fungicide application. More *S. minor* sclerotia were added to the soil after each lettuce crop under furrow irrigation compared with subsurface drip irrigation. Populations of sclerotia increased about fivefold after 3 years of conventional tillage under furrow irrigation and had a less aggregated distribution than with subsurface drip irrigation. Under subsurface drip irrigation, the distribution and number of sclerotia in plots were changed little by minimum tillage practices (58). The suppression of lettuce drop under subsurface drip compared with furrow irrigation is attributed to differential moisture and temperature rather than to changes in the culturable soil fungal, actinomycete, or bacterial populations (10). A random survey of commercial fields under subsurface drip and furrow irrigation in the Salinas Valley confirmed the reduction in lettuce drop under subsurface drip irrigation. Subsurface drip irrigation is a valuable lettuce drop management strategy in areas with no significant amounts of rainfall during lettuce cultivation.

Host resistance. Resistant lettuce cultivars offer the most predictable, convenient, and least expensive option for managing lettuce drop. However, developing resistance to drop in lettuce has been difficult and slow. Currently, no resistant commercial cultivars are available. Resistance to necrotrophic pathogens such as *Sclerotinia* needs to be defined differently because of the involvement of acids and enzymes in pathogenesis. Newton and Sequeira (48) identified several lettuce PI lines that were highly resistant in the field to *S. sclerotiorum* and attributed this to their upright growth habit, as had been determined in beans for resistance (18). Subsequent evaluation of 100 PI lines by Abawi et. al. (2) and nearly 150 PI lines in our laboratory found no association between growth habit and resistance. None of the *L. sativa* accessions screened by Abawi et. al. (2) possessed resistance to *S. minor*.

During our attempts to develop a repeatable resistance screening technique in the greenhouse, we observed a peculiar but interesting phenomenon. While plants in many PI lines died within 24 to 48 h after *S. minor* mycelium appeared at the base of the crown, plants in a small number of lines did not die for nearly 8 to 10 days. This has been named "slow-dying resistance." We determined that instead of identifying PI lines with the smallest percentage of dead plants (low incidence), we should be screening for the factor governing slow-dying resistance (period over which inoculated plants died after the mycelium appeared at the crown). In our evaluation of about 175 PI lines, we have identified 15 lines that possess a stable slow-dying resistance (Table 3). Efforts are currently underway to determine the heritability of this trait and to incorporate this trait into horticulturally acceptable backgrounds.

Other management practices. Other methods such as solarization (27,52) and burning of crop residue (23) reduce *Sclerotinia* inoculum levels, but both methods are impractical in lettuce production because of the climate in California. Because very little lettuce residue is left after a commercial harvest for burning, and overcast skies in the Salinas Valley contribute to air pollution, burning is not an acceptable management practice.

Outlook

Despite the voluminous literature on lettuce drop caused by both *S. minor* and *S. sclerotiorum*, the disease continues to be a major production constraint in most lettuce producing areas, and particularly in California. Research has documented the biological and environmental factors that affect survival, germination, and the ability of *Sclerotinia* spp. to cause lettuce drop under artificially controlled conditions. The conclusions drawn from these studies, however, have not developed into effective and consistent disease management technologies. While subsurface drip irrigation provides economical control of lettuce drop and obviates the need for fungicide use, this type of irrigation technology is expensive and cannot be used in areas that receive rainfall during lettuce cultivation.

Fig. 12. (A) Incidence of lettuce drop under furrow irrigation. (B) Incidence of lettuce drop under subsurface drip irrigation.

Table 3. Reaction of select germ plasm accessions for "slow-dying" resistance to *Sclerotinia minor*

PI number or cultivar[y]	Incidence (%)	Mode (days)[z]	Range (days)
250020	20	6	3-8
169513	20	8	1-15
171665	20	8	6-10
171676	40	8	2-14
172914	60	6	3-12
251246	10	6	6-6
140295	0	…	…
171666	10	5	5-5
171669	10	11	11-11
171671	10	4	4-4
172920	50	7	1-13
174225	40	7	2-14
174229	20	6	3-8
175735	50	6	0-11
176578	60	6	2-21
Batavia Reine de Glacé (control)	80	1	0-4
Salinas (control)	60	1	0-6

[y] One hundred twenty germ plasm accessions and cultivars were screened. Twenty plants from each accession were individually inoculated. The reactions of only the promising lines are presented here along with the susceptible checks.

[z] Days after the appearance of mycelium at the crown when greater than 60% of the plants in the corresponding germ plasm accession died.

Therefore, the identification and development of resistance in lettuce to drop would certainly be considered a Holy Grail. Traditional breeding efforts to date have not resulted in drop-resistant lettuce cultivars. Success in resistance breeding is likely to come from two approaches. First, slow-dying resistance provides a powerful tool to assess resistance to *S. minor* and identify sources of resistance. It is important to determine the heritability of this trait before breeding efforts are directed toward incorporating this characteristic into horticulturally superior backgrounds. Second, for the less specialized necrotrophs such as *Sclerotinia* spp. that have been difficult to control by traditional breeding, success may come from the use of transgenes. Several potentially useful transgenes have already been introduced into lettuce. Currently, however, a rate-limiting step to the deployment of transgenes in lettuce is the loss of phenotype in later generations (46). Once the mechanism underlying this loss of phenotype is understood, rapid progress in breeding resistance to lettuce drop is likely. Until resistant cultivars are available, management of this disease should depend on rotations with crops that actively decrease the number of soilborne sclerotia and integration of other available techniques.

Acknowledgments

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