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Research

Epidemiological Characterization of Lettuce Drop (*Sclerotinia* spp.) and Biophysical Features of the Host Identify Soft Stem as a Susceptibility Factor

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Abstract

The soilborne fungus *Sclerotinia minor* was not known to produce sclerotia in the stems of infected and uncollapsed *Lactuca* standing intact until our observation in a greenhouse in 2017. We investigated lettuce–environment–*S. minor* interactions in two tolerant and four susceptible *Lactuca* genotypes to determine putative risk factors and targets for disease control. Symptomatological, pathophysiological, developmental, basal stem biophysical, and microclimate responses (27 variables) of the genotypes were determined under field or greenhouse conditions. Distinct patterns of infection responses were observed between modern cultivars and their primitive or wild relatives. Modern cultivars were susceptible to rapid basal stem and root degradations by *S. minor*. Oilseed lettuce PI 251246 and wild *Lactuca serriola* 11-G99 were resilient to degradations and significantly deterred mycelium emergence and symptom development but sclerotia formed to a significantly higher height in their stems. Photosynthetic efficiency declined rapidly within 1 day postinoculation (dpi) in susceptible plants but remained intact approximately 5 to 6 dpi in the tolerant 11-G99. Stomatal conductance spiked rapidly in 11-G99 plants within 1 to 3 dpi, coinciding with the emergence of fungal mycelia at the crown. A strong negative correlation detected between basal stem degradation severity or collapse, and stem mechanical strength indicated that stem strength-mediated genetic factors determine the outcome of *Sclerotinia* infections. Soft stem is a prominent lettuce drop susceptibility factor that could be targeted in resistance breeding and provides the prelude for the analysis of the biological basis of plant architecture-mediated resistance to *Sclerotinia* spp. in lettuce and other hosts.

Keywords: carbon assimilation, host resistance, microclimate, pathophysiology, sclerotia, stem mechanical strength, stomatal conductance

Lettuce drop is one of the most economically damaging diseases of lettuce (*Lactuca sativa*) worldwide (Purdy 1979; Subbarao 1998), a crop with a farmgate value in the United States of nearly $2.8 billion (https://data.ers.usda.gov). The disease is caused by two closely related species of the genus *Sclerotinia* (*Sclerotinia sclerotiorum* and *S. minor*) (Leammlen 2001). *Sclerotinia* spp. infect all lettuce types; particularly the leaf, romaine, and head lettuce types (Patterson and Grogan 1985). The two fungal species may coexist in the same production field and, in such fields, lettuce drop is largely caused by *S. minor* (Adams and Tate 1976; Jarvis and Hawthorne 1972). Lettuce drop usually starts as water-soaked lesions at the basal stem, leaves in contact with the soil, or roots at any stage of plant development (Hawthorne 1974; Subbarao 1998). As the disease progresses, the host suffers extensive tissue maceration, girdling of the stem near the ground, wilting of leaves, and collapse within a few days after infection (Subbarao 1998; UC-IPMP 1985). Afterward, the pathogens may survive as active mycelia in infected or dead host plants and on adjacent soil surfaces (Burgess and Hepworth 1996). Sclerotia formed on dead plant parts also may overwinter in the soil for up to 10 years (Boland and Hall 1988; Sherf and MacNab 1986).

Lettuce drop is favored by high relative humidity (RH), excessive soil moisture, high-density planting, and cooler air temperature toward market maturity (Abawi and Grogan 1979; Beach 1921; UC-IPMP 1985). These planting and microclimate conditions impact the survival of sclerotia, their germination, and, ultimately, disease incidence. Rapid lettuce drop development and greater incidence occur at moist soils with RH fluctuating between 80 and 100% and temperature at 20°C (Adams and Tate 1975; type="bibr" rid="B22">Clarkson et al. 2014). The development of *S. minor* is fostered by high soil moisture and temperature ranging from 6 to 30°C (optimal 18°C) (Barrière et al. 2014; Hao et al. 2003). Moist soil conditions after rainfall (7 to 46 mm) in conjunction with 4 to 10 days of daily minimum and maximum air temperatures of 5 to 18 and 14 to 25°C, respectively, resulted in the steady development of lettuce drop caused by *S. minor* (Melzer and Boland 1994). Melzer and Boland (1994) determined that the influence of a crop canopy on temperature, RH, and soil moisture within the crop was minimal.

Sanitation, soil fumigation, deep plowing, crop rotation, irrigation management, protectant chemicals, and biocontrol agents have been used to prevent or manage Sclerotinia diseases, including lettuce drop (Adams and Fravel 1990; Barrière et al. 2014; Ben-Yephet et al. 1986; Chen et al. 2016; Chitrampalam et al. 2008, 2011; El-Tarabily et al. 2000; Leach and Gilbert 1926; Matheron and Porchas 2004; Patterson and Grogan 1985; Rabeendran et al. 2006; Smolińska and Kowalska 2018; Subbarao et al. 1997). The overwintering mechanism and longevity of the pathogen through sclerotia makes it difficult to rely on any single practice to mitigate lettuce drop (Bardin and Huang 2001; Saharan and Mehta 2008; Subbarao 1998). Thus, alternative and sustainable methods of lettuce drop control are required (Hayes et al. 2010; Subbarao 1998). Host plant resistance is an attractive approach because it is convenient, sustainable, and environmentally friendly. However, complete resistance is lacking (Mamo et al. 2019) and lower lettuce drop incidence in some germplasm is often associated with plant developmental traits, including canopy size, seedling vigor, upright growth habit, rapid bolting, and low leaf area (Grube 2004; Grube and Aburomia 2004; Hawthorne 1974; Hayes et al. 2010; Leach and Gilbert 1926; Newton and Sequeira 1972). These characteristics are not commercially acceptable attributes for the leaf, romaine, and head lettuce cultivars on the market.

A host plant resistance mechanism that operates throughout plant development is desirable in cultivated lettuce. However, classical defense against the key pathogenicity factors of *Sclerotinia* spp. is generally limited (Cessna et al. 2000). To date, no genetic source with complete plant resistance to *Sclerotinia* spp. is known (Mbengue et al. 2016). Innate or true physiological resistance is confounded by structural disease avoidance phenotypes; namely, plant density, canopy architecture, flowering time, plant height, maturity, and lodging (Boland and Hall 1987; Kandel et al. 2018; Kim and Diers 2000; Kim et al. 1999; Nelson et al. 1991; Rousseau et al. 2004; Wu et al. 2019). Basal stem diameter has also been implicated in host plant reaction to *S. sclerotiorum* (Li et al. 2006; Porter et al. 2009). Thus, a feasible, resistant-cultivar-based control of Sclerotinia diseases has not been sufficiently developed (Leammlen 2001).

The disease dynamics and the mechanisms of host defense responses against Sclerotinia diseases are poorly understood. Once a *Sclerotinia* sp. comes in contact with the host, it releases oxalic acid (a primary necrotrophic effector) and numerous cell-wall-degrading enzymes to initiate tissue maceration, resulting in water-soaked lesions (Derbyshire et al. 2019; Favaron et al. 2004; Kim et al. 2008; Liang and Rollins 2018; Williams et al. 2011) from the breakdown and degradation of the infected plant tissue (Godoy et al. 1990; Marciano et al. 1983) as the pathogen transitions from a biotrophic to necrotrophic lifestyle (Kabbage et al. 2015). Liang and Rollins (2018) proposed a two-phase infection model in which the pathogen first evades, counteracts, and subverts host basal defense reactions before killing and degrading host cells. Oxalic acid contributes toward both killing and host cell wall degradation (Liang and Rollins 2018).

The pathophysiology (the study of the effect of infection on biological processes) of Sclerotinia diseases on host plants is limited despite their severe impact on seed productivity and germination and oil yield under favorable environmental conditions (e.g., in soybean, bean, and rapeseed) (del Río et al. 2007; Grau 1988; Tu 1989; Venturoso et al. 2015; Willbur et al. 2019). In mint (*Mentha arvensis*) leaves inoculated with *S. sclerotiorum*, reductions in total chlorophyll, phenol, and sugar contents occur (Perveen et al. 2010). In soybean (*Glycine max*) plants infected with *S. sclerotiorum*, reduced photosynthetic efficiency and the corresponding reduction in energy flow by photosystem (PS)II (F_v/F_m) was reported (Vitorino et al. 2020). In cucumber (*Cucumis sativus*) leaves, infection by *S. sclerotiorum* also inhibited photosynthesis by severely damaging the reaction centers of PSII (Bu et al. 2009).

In lettuce, the disease processes triggered by *Sclerotinia* spp. are elusive. *S. minor* was not known to form sclerotia in the stems of infected *Lactuca* plants standing intact in upright positions. *S. minor* was observed to produce sclerotia in the stems of cultivated lettuce well aboveground in a greenhouse in 2017. This and related observations, particularly the absence of rotting of the basal stems and roots of the lettuce genotypes plant introduction (PI) 251246 (*L. sativa*) and 11-G99 (*L. serriola*), prompted us to undertake further investigations. We hypothesized that the phenomena are perhaps related to the fact that these accessions were known to be tolerant of lettuce drop in previous field studies (Grube 2004; Hayes et al. 2010; Subbarao 1998; Whipps et al. 2002). The overall objective of this work was to examine lettuce–environment–*S. minor* interactions to understand the nature and extent of the sclerotia formation and resistance to *S. minor* in *Lactuca* spp. The specific objectives were to (i) assess lettuce drop symptomatology, epidemiology, and variation of *S. minor* sclerotia formation among lettuce genotypes in intact stems aboveground; (ii) identify the symptomatological and pathophysiological

nature of susceptibility and resistance responses; (iii) characterize the relationship of lettuce drop resistance with plant developmental and architecture characteristics (bolting, flowering time, plant height, and basal stem diameter and mechanical strength); (iv) monitor microclimate variations under plant canopy in the field; and, finally, (v) identify possible risk factors for lettuce drop and targets for disease control.

MATERIALS AND METHODS

Plant materials and experimental sites

Six lettuce genotypes (genus *Lactuca*) representing a range of reactions to lettuce drop (*Sclerotinia* spp.) were used for the study (Table 1). The genotypes were Eruption, Reine des Glaces (RG), Salinas, Da Ye Wo Sun (DYWS), PI 251246, and 11-G99. Eruption (PI 613577) is a slow-bolting dark-red Latin-type cultivar exhibiting low disease incidence when exposed to both *S. minor* and *S. sclerotiorum* (Hayes et al. 2010, 2011; Mamo et al. 2019). The cultivar was developed by Enza Zaden (Wehner 2002). RG (PI 634668) is a slow-bolting, light-green, heirloom Batavia-type French cultivar developed by Vilmorin in 1883 (Wehner 2002). Salinas, known as Saladin in Europe, is a slow-bolting crisphead cultivar widely grown since its release in 1975 (Ryder 1979). DYWS (PI 667840) is a Chinese cultivar (called "wosun") grown mainly for its stem (https://npgsweb.ars-grin.gov). Eruption (based on disease severity), RG, Salinas, and DYWS are susceptible to both species of *Sclerotinia*, though they differ in the frequency of dead plants at harvest maturity when grown in fields with a high disease pressure (Hayes et al. 2010, 2011). PI 251246 is an oil-type primitive accession from Egypt (Ryder 1968, 1970) with a large seed used for oil production; it has some level of resistance to both species of *Sclerotinia* (Hayes et al. 2010; Subbarao 1998; Whipps et al. 2002). Genotype 11-G99 is an *L. serriola* (prickly lettuce) line resistant to lettuce drop during spring seasons (in the field) but susceptible during the fall, which appears to be related to its fast bolting in spring plantings and slow bolting in the fall.

Sclerotia formation (and associated symptomatology) and photosynthetic gas exchange and chlorophyll fluorescence evaluation experiments were conducted on plants grown in the greenhouse at the United States Department of Agriculture–Agricultural Research Service (USDA-ARS) in Salinas, CA. Basal stem mechanical strength was assessed on samples collected from greenhouse and field experiments. Disease incidence and microclimate measurements were made on field-grown plants. All experiments were conducted at least two times.

S. minor sclerotia in lettuce stems and symptomatology of disease on host plant

Growth of healthy lettuce plants. Soil mixture SPm (sand/potting mix, 2:1 [vol/vol]) containing regular sand and Premium Growers Mix (Canadian Sphagnum Peat Moss, Forest Products, Perlite) from Sun Land Garden Products, Inc. (Watsonville, CA, U.S.A.) was prepared using a concrete mixer. The SPm was sanitized using a Pro-Grow soil sterilizer (Brookfield, WI, U.S.A.) running at 93°C for 24 h Two lettuce seeds were sown into circular plastifoam cups (473 ml in volume; Amerifoods Trading Co., Los Angeles, CA, U.S.A.) containing 450 g of the soil mixture. Plants were grown on greenhouse benches (20 to 25°C day, 15 to 17°C night) without supplemental lighting until the end of experiments. Plants were watered as needed and thinned to one plant per pot when they were 2 weeks old. They were fertilized every 14 days with Miracle-Gro (The Scotts Company, Marysville, OH, U.S.A.), a nutrient solution with N-P-K fertilizer (15-30-15), at approximately15 ml/pot, prepared according to the manufacturer's instructions. The experiments were set up in a completely randomized design with three replications and 10 plants in each replication for each genotype. Ten plants were grown as controls for each genotype. The plants were monitored for flowering. Plant height and basal stem diameter (approximately 2.5 cm above the soil surface) were measured at inoculation (Table 2).

Inoculum preparation. A mixture of sclerotia of four isolates of *S. minor* (BM001, BM004, BM005, and BM010), collected from infected lettuce from four different fields in the Salinas Valley, CA, was used for the experiments. The fungal cultures were grown on Petri dishes containing sterile, plain potato dextrose agar (PDA) for 3 to 4 days. Rye seed was soaked in 250 ml of distilled water for two nights, then autoclaved at 121°C for 20 min, twice. Then, one disk (approximately 6 mm in diameter) of the mycelial plug was removed from the margin of advancing colonies of 3-day-old *S. minor* culture of each of the four isolates on a PDA plate and was added to 50-ml jars containing 10 g of the autoclaved rye seed plus 10 ml of sterile distilled water. The fungal disks were gently mixed with the rye seed to ensure maximum seed

TABLE 1

Lactuca genotypes evaluated for reaction to lettuce drop, host plant architecture, and microclimate conditions under plant canopy with their bolting rating and reaction to *Sclerotinia minor*

Genotype	Horticultural type or species[x]	Bolting rating (1 to 7 score)[y]	Field reaction to *S. minor*[z]
Eruption (PI 613577)	Latin	1.29	0.28
Reine des Glaces (RG, PI 63466)	Batavia	1.00	0.91
Salinas	Crisp	1.00	0.68
Da Ye Wo Sun (DYWS, PI 667840)	Stem	3.75	0.61
PI 251246	Oil	6.33	0.27
11-G99	*Lactuca serriola* L.	3.17 (2.00)	0.19 (0.60)

[x] All genotypes but 11-G99 are *Lactuca sativa*; 11-G99 belongs to the wild relative *L. serriola*. For this study, Eruption and Reine des Glaces are considered as leaf lettuce; Salinas is crisphead lettuce; Da Ye Wo Sun is stem lettuce; PI 251246 is oil-seed lettuce; and 11-G99 is prickly lettuce.

[y] Scores: 1 = no bolting, 4 = moderate bolting, and 7 = rapid bolting. Genotype 11-G99 is a photoperiod-sensitive *L. serriola* that bolts rapidly in the spring season (score 3.17) and slowly during the fall (score 2.00). Mean scores from four experiments are provided for the other genotypes.

[z] Mean disease rating scores (arcsine square root transformed disease incidence data) from four experiments are presented. Eruption and PI 251246 are tolerant (moderately resistant); Salinas, Reine des Glaces, and Da Ye Wo Sun are susceptible; and 11-G99 is moderately resistant in the spring season (score 0.19) and susceptible during the fall season (score 0.60).

TABLE 2

Developmental, symptomatological, physiological, basal stem biophysical, and microclimatic features of *Lactuca* spp. measured to characterize a new disease phase in the disease cycle of lettuce drop and identify features associated with resistance to *Sclerotinia* spp.

Name	Data description	Purpose
Days to 50% flowering	Number of days from planting to approximately 50% flowering of each plant	This dataset was used to analyze how flowering time relates to lettuce drop and host resistance
Plant height (cm)	Length of each plant from the base to the shoot tip	This dataset was used to analyze the within-genotype variation of symptom development
Basal stem diameter at inoculation (mm)	It provides the mean of three measurements of the perimeter of the stem approximately 25 cm aboveground using a digital caliper	This dataset was used to assess whether the diameter impacts symptom development
Days to mycelium emergence	Number of days postinoculation (dpi) it took the *S. minor* to initiate the first sign of infection, the growth of mycelium, at the base of the stem	This dataset was used to analyze the difference among genotypes in the number of days to mycelium emergence at the basal stem
Days to cortex softening	The number of dpi it took for the *S. minor* to initiate softening or discoloration at the base of the stem tissue	This dataset was used to analyze the difference among genotypes in the number of days to cortex softening postinoculation
Days to collapse	Number of dpi for the plant to collapse (fall off) due to infection at the base of the stem	This dataset was used to analyze the difference among genotypes in the number of days to collapse postinoculation
Proportion collapsed	Data were expressed as the number of plants collapsed over the total number of inoculated plants	This dataset was used to analyze the difference among genotypes in the proportion of plants collapsed due to lettuce drop
Collapse rating	Arcsine square root transformation of the proportion of plants collapsed due to infection	The data were used to achieve normality of data distribution
Days to lower leaf discoloration	Number of dpi for the plant to show discoloration of lower leaves	This dataset was used to analyze the difference among genotypes in the number of days to lower leaf discoloration postinoculation
Days to leaf wilting	Number of dpi for the plant to show wilting of leaves	This dataset was used to analyze the difference among genotypes in the number of days to leaf wilting postinoculation
Days to shoot wilting	Number of dpi for the plant to show the beginning of shoot wilting	This dataset was used to analyze the difference among genotypes in the number of days to shoot wilting postinoculation
Days to mortality	Number of dpi for the complete death (total termination of active growth) of the whole plant to occur	This dataset was used to analyze the difference among genotypes in the number of days to mortality postinoculation
Lesion length (weekly; cm)	Length of water-soaked, light-brown discolored patches on stems; measured weekly	This dataset was used to analyze the difference in (weekly) lesion length among genotypes after infection
Lesion length (final; cm)	Lesion length at final evaluation for sclerotia formation aboveground	This dataset was used to analyze the difference among genotypes in lesion size preceding mortality
Area under lesion progress curve (AULPC)	Lesions lengths of the first five weeks (after infection) were used to calculate the AULPC for each genotype	This was used to quantify the intensity of lesion development over time
Days to evaluation for sclerotia formation	Number of dpi until evaluating each plant for sclerotia formation aboveground	Determines whether the genotypes vary in days to evaluate for sclerotia formation
Cortex degradation length (completely; cm)	Length of the cortex that is completely degraded (likely by cell wall degrading enzymes)	Determines whether the cortex is involved in lettuce drop infection or resistance
Cortex degradation length (partially; cm)	Length of the cortex that is partially degraded	
Basal stem degradation length (cm)	Length of the basal stem highly degraded by the fungus as indicated by shredded symptoms at the soil-basal stem interface	Provides evidence of whether genotypes differ in reaction to infection
Height to which sclerotia formed externally (cm)	Height to which sclerotia is visible outside of the cortex aboveground	Provides the height to which sclerotia formed aboveground outside of the cortex
Height to which sclerotia formed internally (cm)	Height to which sclerotia is visible at the pith aboveground	Provides the height to which sclerotia formed aboveground inside the pith and determines variation among genotypes
Pith degradation height (completely; cm)	Length of the pith completely degraded	Enabled determination of the relative importance of pith in infection or resistance
Pith degradation height (partially; cm)	Length of the pith that is partially degraded	
Internal discoloration height (completely; cm)	Length of the internal part of the stem (i.e., pith) that is completely discolored likely due to pathogenicity factors (e.g., toxins) produced during infection	Was used to assess the possible difference among genotypes in the discoloration symptom developed inside the pith

(*Continued on next page*)

TABLE 2

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Name	Data description	Purpose
Internal discoloration height (partially; cm)	Length of the internal part of the stem (i.e., pith) that is partially discolored likely during the process of infection	
Root degradation severity	Extent of root system degradation denoted as scores (i.e., no degradation or intact = 0; partially degraded = 0.5; completely degraded = 1) due to lettuce drop	Enabled the comparison of the genotypes based on the severity of root degradation
Net carbon assimilation rate (A; μmol CO_2 m^{-2} s^{-1})	Estimate of net carbon assimilated during photosynthesis (LI-COR Biosciences 2011); the measure of the incorporation of carbon from atmospheric CO_2 into organic molecules $A = \frac{F\,(C_r - C_s\,(\frac{1000-W_r}{1000-W_s}))}{100S}$ where: • C_r and C_s are measurements of CO_2 concentrations from the reference CO_2 supply and leaf sample • W_r and W_s are measurements of mole fractions of reference and leaf sample water vapor • F is the airflow rate • S is the leaf area	A was used to assess the effect of infection on the rate of photosynthesis and the general health of the plant
Stomatal conductance (g_s; mol H_2O m^{-2} s^{-1})	An estimate of the stomatal conductance to water vapor (LI-COR Biosciences 2011); the measure of the degree of stomatal opening (i.e., rate of passage of CO_2 entering, or water vapor exiting through the stomata) of a leaf and can be used as an indicator of plant water status (Gimenez et al. 2005) $g_s = \frac{1}{\frac{1}{g_{tw}} - \frac{k_f}{g_{bw}}}$ where: • g_{tw} is the total conductance to water vapor, incorporating measurements of W_r and W_s as defined above • k_f is an estimate of the fraction of stomatal conductances of one side of the leaf to the other • g_{bw} is the boundary layer conductance to water vapor	Values of the g_s were used to assess xylem health and function, as well as a general stress response
Photochemical quenching (qP): the proportion of open photosystem (PS)II, the central enzyme in photosynthesis	Coefficient of photochemical fluorescence quenching; a measure of the rate at which electrons are transported away from PSII due mainly to the light-induced activation of enzymes involved in photosynthesis (Maxwell and Johnson 2000). PSII is a multifunctional complex of protein-pigments that is comprised of water-splitting components, light-harvesting complexes, and a reaction center (Jordan 1996) $qP = \frac{Fm' - F}{Fm' - Fo'}$ where: • F_m' is the maximal fluorescence yield induced by a saturating light pulse which temporarily closes all PSII reaction centers • F is the fluorescence yield before the application of a saturating light pulse • F_o' is the minimum fluorescence level in the dark following a saturating light pulse	qP represents the proportion of PSII reaction centers that are open and ready to receive light for photochemistry; used to measure the health of the light-harvesting systems
Chlorophyll index	Chlorophyll content based on the absorbance of the leaf at 650 nm and 940 nm using a Soil Plant Analysis Development (SPAD) 502 Plus Chlorophyll Meter (https://www.specmeters.com) (Uddling et al. 2007)	Chlorophyll concentrations were measured to assess symptoms of the disease on the leaves

(*Continued on next page*)

TABLE 2
(*Continued from previous page*)

Name	Data description	Purpose
Cortex strength (g of force)	Mechanical strength of the "skin" of the basal stem tissues	Was used to assess the possible role of the cortex tissue in resistance
Xylem strength (g of force)	Mechanical strength of the xylem tissue of the basal stem	Enabled determination of the possible role of the xylem tissue in resistance (perhaps as a physical barrier)
Pith strength (g of force)	Mechanical strength of the pith tissue of the basal stem	Used to assess the possible role of the the central parenchyma cells in the stem in resistance
Basal stem diameter at strength evaluation (mm)	Provides the perimeter of the basal stem tissue used for stem mechanical strength measurement	Was used to assess whether the basal diameter impacts symptom development
Disease incidence	Data were expressed as the number of plants showing lettuce drop symptoms over the total number of inoculated plants	Data were used to determine the difference in lettuce drop resistance among accessions
Disease rating	Arcsine square root transformation of the proportion of plants died due to infection; unless otherwise noted, disease rating is presented about lettuce drop in this article	Data were used to achieve normality of data distribution
Standardized area under the disease progress stairs (sAUDPS)	sAUDPS score was calculated from a weekly proportion of mortality evaluations (Simko and Piepho 2012)	Data standardize the disease incidence measured weekly
sAUDPS residual	Residual resistance score calculated from the sAUDPS regressed on the bolting score (Mamo et al. 2019)	Data provide resistance scores remaining after removing the portion of resistance contributed by the rate of bolting
Disease severity index (DSI)	Data are derived from disease severity scores based on a scale of 1 (no degradation) to 5 (complete degradation) of the basal stems of infected or dead plants (see below)	Data provide the extent of basal stem degradation of infected or dead plants
Rate of bolting	The relative rate of emergence of a stalk (or stems) and flowering organs	Used to assess the relative impact of bolting on lettuce drop resistance
Relative humidity, RH (hourly; %)	RH under plant canopy measured every hour from the onset of lettuce drop to harvest maturity of the host plant	Data were used to assess whether RH plays a major role in lettuce drop development
Temperature (hourly; °C)	Temperature under the plant canopy measured every hour from the onset of lettuce drop to harvest maturity of the host plant	Data were used to assess whether temperature plays a major role in lettuce drop development

colonization. The flasks were incubated at room temperature for 3 to 4 days and used for inoculation before sclerotia were formed.

Inoculation and disease development. To ensure that the effects on lesion size and pathogen susceptibility were compared at the same developmental stage, each genotype was inoculated when plants reached approximately 50% flowering. Reaction to *Sclerotinia* spp. in lettuce is usually confounded with bolting. Assessment at the flowering stage allows detection of the differences in symptom development among genotypes with varied rates of bolting. For inoculation, 10 infested rye seeds (visually determined to have been colonized by mycelia) were placed just under the soil surface adjacent to the basal stem of each plant (Adams and Tate 1976). Each experiment included 30 plants per genotype, and plants were inoculated in groups of 6 to 30 per test, for a total of 24 separate tests between the two experiments. In a few instances where the first inoculum failed to produce actively growing mycelium at the basal stem, plants were reinoculated with approximately five colonized rye seeds to ensure successful infection. For controls, 10 plants per genotype were treated with healthy rye seed. After inoculation, the pots were watered gently, maintained inside the greenhouse, and monitored for multiple symptoms.

Symptomatology of lettuce drop and associated variables. Inoculated plants were individually monitored (daily) and evaluated for the emergence of mycelium and the first appearance of *Sclerotinia*-induced water-soaking symptoms. Following the appearance of mycelial growth at the basal stem, plants were evaluated for visual symptom-related variables (annotating the speed of appearance and symptom intensity) daily or weekly until mortality (Table 2).

Evaluation for sclerotial formation aboveground. The height to which sclerotia formed aboveground (from the soil surface) in or on the stem of each plant was measured after the plant completely dried. The samples were also evaluated for the appearance of additional signs and symptoms on both the aboveground plant parts and the root system. All measurements are detailed in Table 2. The evaluations for sclerotia formation and lettuce drop symptomatology were conducted over two time periods in greenhouse experiments 1 (March to October 2017) and 2 (September 2017 to April 2018) (hereafter gh1 and gh2).

Photosynthetic gas exchange and chlorophyll fluorescence measurements. Four physiological traits (carbon assimilation or photosynthetic efficiency, stomatal conductance, photochemical quenching or chlorophyll fluorescence, and chlorophyll index) (Table 2) were evaluated on some of the same plants used for lettuce drop symptomatology. Carbon assimilation (*A*) and photochemical quenching (*qP*) were measured using a LI-COR 6400XT Portable Photosynthesis System (LI-COR Biosciences, Lincoln, NE, U.S.A.) for 3 to 32 plants of genotypes with rapid (Salinas) and prolonged (11-G99) responses to infection during gh2. Immediately following measurements using the LI-COR, chlorophyll fluorescence was measured using a Walz Mini-PAM Portable Chlorophyll Fluorometer (Heinz Walz GmbH Mess- und Regeltechnik, Eichenring, Effeltrich, Germany). Relative chlorophyll concentration was measured nondestructively using a SPAD 502 Plus Chlorophyll Meter (Spectrum

Technologies, Aurora, IL, U.S.A.). Three leaves were evaluated for all measurements on each plant from old, middle, and young leaves, and an attempt was made to evaluate the same leaves every day. All measurements were taken between 11:00 A.M. and 3:00 P.M. on each day; preliminary 24-h measurements of *A* suggested that plants reached maximum levels during this time of the day under greenhouse conditions. Light response curves suggested peak *A* between 800 and 1,000 μmol m^{-2} s^{-1} for *L. sativa* 'Salinas' and between 1,000 and 1,200 μmol m^{-2} s^{-1} for *L. serriola* accession US96UC23 (Eriksen et al. 2020). Light intensity was set to 800 μmol m^{-2} s^{-1} because the plants were acclimated to the low ambient light conditions of the greenhouse (mean 134 μmol m^{-2} s^{-1} ± 61 standard deviation). The infrared gas analyzers were matched every 30 min using settings previously described (Eriksen et al. 2020).

Lettuce basal stem mechanical strength evaluation. The basal stem strength was evaluated using the TA.XTplus Texture Analyzer (Texture Technologies Corp., Hamilton, MA/Stable Micro Systems, Godalming, Surrey, U.K.) following the manufacturer's instructions (Supplementary Fig. S1A). Ten plants of each accession were grown in the greenhouse, as described previously, in a completely randomized design with two replications. When the plants reached approximately 50% flowering, their basal stems were harvested for phenotyping by cutting approximately 0.5 cm belowground. The mechanical strength measurements were taken immediately afterward between 0.5 and 1.0 cm from the edge of the basal stem; the common site of symptom initiation caused by myceliogenic germination (Patterson and Grogan 1988) (Supplementary Fig. S1B). The strength of each basal stem was measured twice from different orientations and the mean was used in further analyses. A computer macro was developed to generate the separate strength of each of the three layers of stem: cortex, xylem, and pith (Table 2; Supplementary Fig. S1C and D). Pith is the soft, spongy tissue composed of parenchyma cells at the center of the stem. The measurements and data analysis were aided by the Exponent Connect software v. 6.1.16.0 (Stable Micro Systems). The basal stem diameter of each stem sample was generated using a function incorporated into the software. The experiment was conducted twice. To determine the consistency of basal stem strength across locations, we also evaluated stem samples of the same accessions grown in the field in 2017 (fall season). Two plants each from two replications were obtained at harvest maturity and evaluated for strength following a protocol like that of the samples from the greenhouse. The mean of the strength for each plant in each replication was used in further analyses.

Evaluation of resistance to lettuce drop and rate of bolting. The six lettuce accessions and the susceptible commercial romaine cultivars as controls (Brave Heart, Green Forest, and Hearts Delight) were evaluated for resistance to lettuce drop and rate of bolting in both spring and fall 2016 and 2017 (hereafter spr16, spr17, fall16, and fall17), as previously described (Hayes et al. 2010, 2011; Mamo et al. 2019). Briefly, the six lettuce accessions were grown in the field at the USDA-ARS Station in Salinas, CA. Plots were infested with the sclerotia of *S. minor* just before planting in the spring experiments; mycelium from germinating sclerotia in the soil from the previous season served as inoculum for the fall experiments as a standard practice at the site (Hayes et al. 2010, 2011; Mamo et al. 2019). Lettuce drop incidence was recorded weekly from the first disease onset to harvest maturity. Disease incidence and disease ratings were used in analyses (Table 2). Lettuce drop severity was also measured weekly, during the fall17 experiment, based on the severity of degradation at the basal stem using a newly developed scale of 1 to 5 (Tables 2 and 3; Fig. 1). The disease severity scores were used to calculate the disease severity index (DSI) of each plot as follows:

$$\text{Disease severity index (DSI)} = \left[\sum_{i = 1,\ 2,\ 3,\ 4,5} (S_i{*}N_i)/5T) \right] {*} 100$$

where S_i is the appropriate basal stem degradation class from 1 to 5, N_i = number of the diseased or symptomatic plants in the ith class, and T = the total number of plants rated 1 to 5 in each plot. Per plot, the DSI ranged from 0 (no disease) to 100 (all plants rated had completely degraded basal stems or had fallen off due to disease). Some plots were coded as missing data while generating the mean DSI. The proportion of plants collapsed due to infection (i.e., the number of degraded or collapsed plants from the total number of plants infected) may also be considered as a "degradation severity" phenotype.

The extent of bolting (stem elongation or plant development) was evaluated at harvest maturity on a scale of 1 to 7, where 1 = rosette, no stem, or no internode; 2 = internode beginning to emerge; 3 = bud beginning to emerge; 4 = expanded inflorescence with buds and branches between them; 5 = first flower emerged; 6 = more than 50% flowering occurred; and 7 = first fluff or open involucres with fluff beginning to emerge from the seed.

Effect of temperature and humidity on lettuce drop incidence. The effect on lettuce drop of RH and temperature under the plant canopy were monitored using Maxim Integrated DS1923-F5# iButton data loggers (iButtonLink Technology, Whitewater, WI, U.S.A.) on plants grown in the lettuce-drop-infected field in spr17 and fall17. The DS1923-F5# is a high-resolution Hygrochron sensor containing a complete humidity and temperature logging system for applications in environmental studies (Fawcett et al. 2019). The iButtons were set to record humidity and temperature every hour from the first lettuce drop onset to harvest maturity with no rollover and high resolution using the DS1402D-DR8+ Blue Dot Receptor and the temperature logging and reporting software Thermodata Viewer (v. 3.2.12; Thermodata Corporation, Milwaukee, WI, U.S.A.). To prevent the sensors from direct contact with moisture, they were covered with a moisture-wicking fabric, without interfering with the humidity aperture, and placed in proximity to the basal stem of a plant at the center of the row in three replications for each accession in both seasons. All iButtons were placed under leaves at the west side of individual plants to control for possible variations caused by the orientation of placement. Additional data loggers were placed in the field as controls at three locations devoid of lettuce or other plants. The plants housing the iButtons were monitored for mortality (daily) and the corresponding sensor was moved to a healthy neighboring plant when the original plant died, recording the date of relocation. At the end of the experimental period, the iButtons were retrieved from the field, and data were downloaded using the Thermodata Viewer software along with the Blue Dot Connector. The average temperature and RH and data corresponding to the weekly disease measurements were used in data analyses.

Statistical analysis. Each dataset was checked for normality. Box-Cox transformations (Box and Cox 1964) were performed when residuals were not normally distributed, and the datasets permitted transformations. Arcsine square root transformation was performed on a proportion variable to achieve tests of normality. After the transformations, the normality of the datasets was rechecked and confirmed with normal probability

plots; homogeneity of variances was also ascertained using Levene's test. All data were analyzed by analysis of variance for each experiment, whenever the datasets permitted, using a linear mixed-effects models approach using the R software package (R Core Team 2019). Significant differences among genotype means within each measured parameter were determined through pairwise comparisons of least square means (α = 0.05). The individual experiments included replicates and genotypes; genotype was considered as a fixed effect and the replicates as random effects.

For the physiological traits (photosynthetic gas exchange and chlorophyll fluorescence) measured in this study, data were evaluated for normality and homoscedasticity using Shapiro.test {stats} and Levene.test {lawstat} (Levene 1960; Shapiro and Wilk 1965). Outliers were identified using boxplots but not removed from the dataset unless they represented obvious errors introduced by a miscalibration of the photosynthesis system. The data were transformed for normality and homoscedasticity to conform to the assumptions of parametric tests, or a Kruskal Wallis nonparametric test was performed (Kruskal.test {stats}) (Kruskal and Wallis 1952). *P* values generated using the Kruskal-Wallis tests are presented for significant differences between genotypes because both parametric and nonparametric runs produced similar results.

Predicting resistance to* Sclerotinia *spp. in lettuce. Regression analyses were used to investigate the risk of lettuce drop development because of inherent host plant characteristics and microclimatic conditions under the plant canopy. In the analysis of greenhouse experiments, eight parameters (collapse rating, days to mortality, basal stem degradation length, height to which sclerotia formed externally and internally, partial pith degradation, internal discoloration heights, and root degradation severity) were selected as response variables based on the consistency of the pairwise Pearson correlations across the two experiments. Of all the possible candidates as predictors, parameters highly correlated with the (selected) response variables and least correlated with each other were selected for assessment of their predictive powers. Variables of focus for analysis of data from the field were (i) those highly correlated with DSI or disease rating, as indicated by the significance of their Pearson correlation coefficients, and (ii) those that showed the least multicollinearity (based on the pairwise Pearson correlations). Accordingly, the effects of plant development and architecture (bolting rate, days to flowering, plant height, and basal stem diameter), basal stem strength (xylem), and microclimate (RH and temperature) conditions on lettuce drop incidence or rating and DSI were analyzed for their predictive powers.

Once the variables of focus were identified, ordinary least squares regression was run to estimate the explanatory

TABLE 3

Scale developed to rate basal stem degradation (i.e., lettuce drop severity) after infection by *Sclerotinia* spp.

Scale (degradation class)[z]	Corresponding infection response	Characteristics				Remarks
		Infection of plant (signs and symptoms)	Mortality	Degradation at the basal stem	Stem tissue maceration	
0	Not applicable	No; plant completely healthy (no sign or symptom)	Not applicable	Not applicable	Not applicable	For susceptible genotypes, only a few plants remain uninfected at the end of the growing season
1	Resistant (R) to degradation	Yes and No; may get an infection with very small lesions at the basal stem or base of lateral branches showing symptoms (no sign on the main stem)	No and Yes; may die slowly ("slow dying")	No; no visually detectable degradation; the entire root system (taproot with lateral roots with hairs) comes out when uprooted	No	Symptoms – yes; small lesions at the base of main stems (perhaps 'resistance response?'); lateral branches may show signs (mycelium and sclerotia)
2	Moderately resistant (MR) to degradation	Yes; signs (mycelium and sclerotia) conspicuous at the basal stem	Yes	No on the main stem (degradation may occur belowground or at the base of lateral branches; taproot comes out when plant pulled out)	No (root tissue maceration or root hair degradation may occur); the main stem may succumb to tissue maceration at the basal stem and 'collapse' but no degradation of the "second stem layer" (xylem tissue)	Symptoms – yes; signs at the basal stem of the primary plant
3	Moderately susceptible (MS) to degradation	Yes	Yes	Yes – partial; detaching stem from the root at the basal stem (point of infection) requires more force; in most cases, taproot does not come out when the plant pulled out; root hair lost	Yes; medium-sized maceration; basal stem may collapse due to maceration and severe degradation of the entire layer at the base	Symptoms – yes; lesions on main stem resulting in degradation or plant death
4	Susceptible (S) to degradation	Yes	Yes	Yes – mostly; collapse with little push or pull force	Yes; long and severe stem tissue maceration	Symptoms – yes
5	Highly susceptible (HS) to degradation	Yes	Yes	Yes; complete degradation or self-collapse	Yes; complete maceration	Symptoms – yes

[z] Rating 0 was included for reference and is not part of the scale.

parameters. Stepwise regression and best subsets regression procedures were employed for variable selection. For regression models with a few variables, a partial *F* test (with "anova") and the likelihood ratio test (with the "lmtest" function) were used to compare the statistical significance of the subset and the full models. For models with several variables, the "leaps" package in R was executed to exhaustively search all subset models (Lumley 2020). The metrics (adjusted) coefficient of determination (R^2) (Wright 1921), Bayesian information criterion (Schwarz 1978), Mallows's Cp (Mallows 1973), or regression sum of squares (Archdeacon 1994) were used as a guide in model selection. The R^2 was used as a measure of the amount of variability in a response variable explained by a univariate model. For multiple regression models, the adjusted R^2 was used as a coefficient of determination. The final model comprises the best predictors from the host plant characteristics or the microclimate conditions.

RESULTS

A new disease phase caused by *S. minor* in lettuce

Production of sclerotia in the stems of the lettuce accession PI 251246 (*L. sativa*) was first observed in a greenhouse at the USDA-ARS, Salinas, CA in March 2017 (Fig. 2A and B). A similar observation was made a few days later on 11-G99 (*L. serriola*). The sclerotia formation was observed primarily inside piths and cavities of stems of both accessions; sclerotia infrequently formed on the outer surface of the stems. The dead 11-G99 plants did not show any visible symptoms of decay from lettuce drop (Fig. 2C). The belowground parts (root systems) of the dead plants were also completely intact; there was no sign or symptom of lettuce drop or rotting on or inside the roots. Exploration of additional genotypes revealed the production of sclerotia in the stems of leaf lettuce types (e.g., RH15-0332; an RG × Eruption recombinant inbred line [RIL]; $F_{6:8}$) approximately a month later in April. The RH15-0332 plant had little to no decay of the basal stem but had a bleached stem harboring sclerotia inside the pith. Another RG × Eruption RIL (RH15-0402) evaluated on 8 April 2017 had no sclerotia in the stem and showed no bleaching symptom associated but exhibited degradation of the basal stem and root system. This provided the first insight into the possible existence of variation among lettuce genotypes in the production of sclerotia in the stem. The appearance of white fungal mycelium on the basal stem and dead plant debris coupled with diagnosis in the laboratory confirmed that all these plants were infected by *S. minor*. Lettuce plants of all types are generally evaluated for lettuce drop at physiological maturity before

FIGURE 1
Scale (1 to 5) developed to rate basal stem degradation (i.e., lettuce drop severity) after infection by *Sclerotinia minor*, where 1 = the plant is wilting and the basal stem or base of lateral branches exhibit symptoms of very small lesions. It is considered resistant (R) to degradation. Rating 2 = signs (mycelium and sclerotia) conspicuous at the base of the main stem with possible tissue maceration; it is considered moderately resistant (MR) to degradation. Rating 3 = signs visible at the basal stem along with medium-sized maceration and partial degradation; it is considered moderately susceptible (MS) to degradation. Rating 4 = signs observed at the basal stem along with long and severe stem tissue maceration and degradation; it is considered susceptible (S) to degradation. Rating 5 = complete basal stem tissue maceration and degradation; it is considered highly susceptible (HS) to degradation. Rating 0 was included for reference; it represents completely healthy plants (i.e., no symptom).

harvest and seldom at senescence or in the stem, precluding the identification of this phase of the disease previously. Complete degradation and decays of the basal stem (and root) and collapse were typical symptoms of lettuce drop exhibited by known commercial cultivars such as Salinas (Fig. 2D).

Formation of sclerotia of *S. minor* in lettuce stems and visual symptoms

In both greenhouse experiments, the control plants treated with noninfested rye seed did not show any sign or symptoms of lettuce drop. Plants (especially modern cultivars) inoculated with *S. minor* showed various visual symptoms (Tables 2 and 3; Supplementary Table S1). Assessments of each genotype revealed discrete patterns of symptom development between cultivated and primitive or wild relatives.

The six accessions showed significant variations for most of the visual symptoms monitored in gh1 and gh2 (Tables 4, 5, and 6). The modern leaf- or head-type (Eruption, RG, and Salinas) and stem-type (DYWS) cultivars had shorter incubation periods than PI 251246 and 11-G99. The former cultivars (susceptible group) all had significantly fewer days postinoculation to mycelium emergence, lower-leaf discoloration, leaf or shoot wilting, and mortality compared with PI 251246 and 11-G99 in both experiments ($P < 0.001$). Plants of the susceptible cultivars exhibited lower-leaf discoloration (and wilting) within 4 (and 5) days postinoculation (dpi), whereas tolerant genotypes took 8 (and 11) days to show leaf discoloration (and wilting), respectively. The modern cultivars also had significantly higher root degradation severity than PI 251246 and 11-G99, with 60% of plants collapsed within a few days postinoculation. No plant of accession PI 251246 or 11-G99 collapsed.

Effect of lettuce drop on gas exchanges (photosynthetic efficiency)

A significant difference in *A* rates between 11-G99 and Salinas plants was recorded during each day of measurements ($P \leq 0.008$). In the susceptible genotype (Salinas), a rapid decline in net *A* rate was evident within 24 h postinoculation (hpi) in contrast to 11-G99 (Fig. 3A). In Salinas, *A* declined severely to respiration levels at 4 dpi. In 11-G99, *A* was intact until approximately 5 to 6 dpi and did not reach respiration levels even on the last day of the experiment (10 dpi). This is consistent with the fact that 11-G99 took significantly more days to show lower-leaf discoloration and wilting compared with Salinas (Table 3). Plant height and the *A* rate in the upper leaves were positively correlated during late stages of infection in 11-G99 ($r = 0.59$, $P < 0.001$), suggesting that time to mortality is related, in part, to the time required for the effect of the infection process to reach the top of the plant. A spike followed by a rapid drop in stomatal conductance was recorded in 11-G99 shortly after inoculation, in the upper and middle leaves, before the decline in *A* began (Fig. 3B).

Phenotypic variation for basal stem mechanical strength

The lettuce genotypes showed statistically significant variation in basal stem biophysical characteristics (xylem, pith, and cortex strengths) (Table 7). PI 251246 and 11-G99 had stronger xylem tissues than Eruption, RG, Salinas, and DYWS. There was a nearly twofold difference in mean for the trait between PI 251246 and 11-G99 and the remaining genotypes in almost all genotype ± experiment combinations (6,914 ± 2,492 versus 2,696 ± 977 g of force, respectively). PI 251246 and 11-G99 had a similar xylem strength in both the greenhouse and field experiments, except that 11-G99 from the field (determined in fall17) had significantly

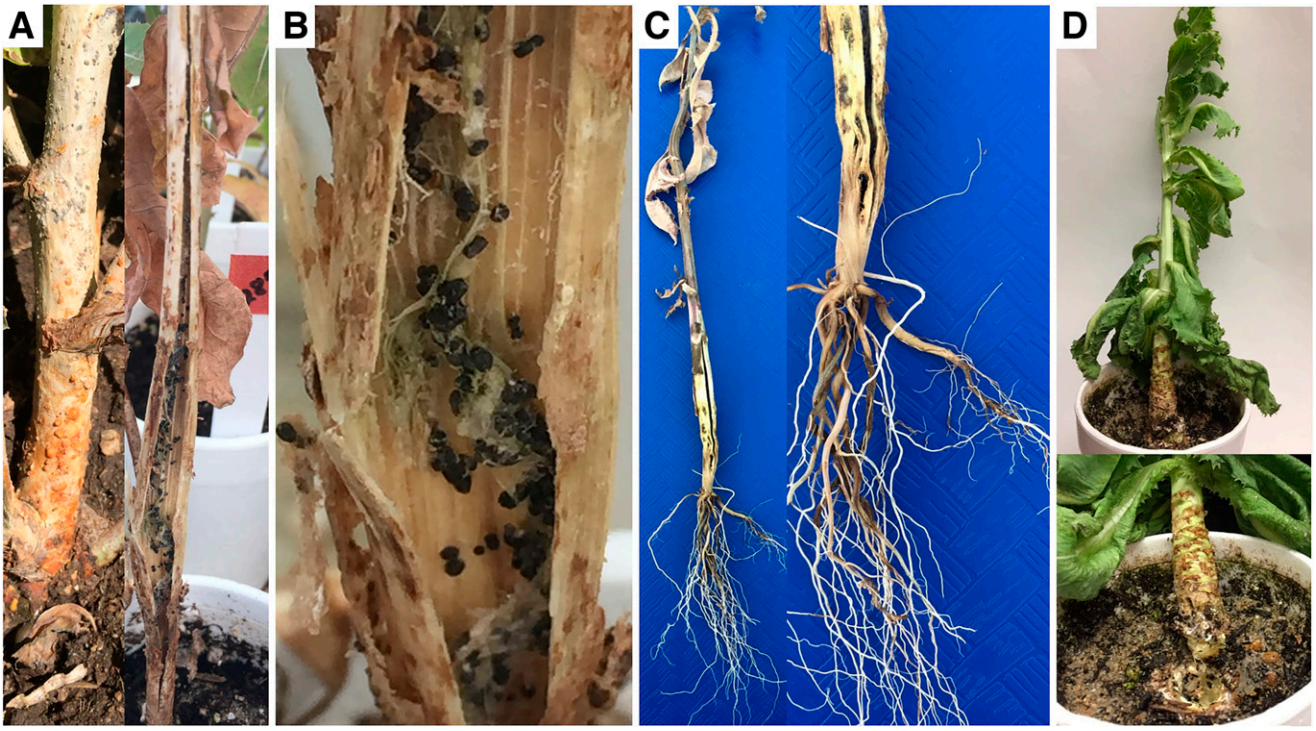

FIGURE 2
Lettuce genotypes **A,** PI 251246 infected by lettuce drop (*Sclerotinia minor*) and exhibiting sclerotia formed aboveground on the stem cortex and in the pith; **B,** close up of sclerotia inside the pith cavity; **C,** 11-G99 infected with *S. minor* but retained intact basal stem and root tissues; and **D,** collapsed cultivar Salinas plant a few days after infection with *S. minor.*

lower xylem strength as it bolted late in the fall. The latter suggests that stem strength is (positively) associated with the rate of bolting, at least in 11-G99 (see below). Genotype 11-G99 from the fall17 field experiment had a basal stem strength in all three components (xylem, pith, and cortex) similar to that of the modern cultivars (Table 7). PI 251246 and 11-G99 also had higher pith strength than the other genotypes. No variation was observed in cortex strength among the six genotypes. The four modern cultivars had statistically similar xylem, pith, and cortex strengths from both the greenhouse and field. Lettuce genotypes with weaker xylem strength were all at significantly higher risk of *Sclerotinia*-triggered basal stem degradation (and collapse) and exhibited higher root degradation severity (see above). The four genotypes with softer xylem had shorter pith degradation heights compared with the two accessions with stronger xylem.

Phenotypic variation for resistance to lettuce drop and bolting in the field

The (susceptible) romaine cultivars included as controls reacted as expected during all four lettuce drop experiments in the field with higher disease incidence; they also had higher DSI (in fall17). The test entries Eruption and PI 251246 had the lowest mean disease (incidence) measurement values, whereas Salinas, RG, and DYWS did not significantly differ from the susceptible controls (Table 8). In terms of disease severity, the average DSI ranged from 42 (PI 251246) to 100 (11-G99). PI 251246 had the lowest mean DSI that significantly differed from all other genotypes. Eruption had a DSI similar to the susceptible genotypes, just like 11-G99 in the fall, indicating that the pathogen uses a mode of infection that is similar in Eruption and the susceptible genotypes. Genotype 11-G99 had mean disease measurements that fell between the resistant and susceptible genotypes due to its susceptibility during both fall16 and fall17 seasons. Eruption, RG, Salinas, and the control cultivars had a statistically similar lowest rate of bolting that differed from DYWS, PI 251246, and 11-G99, suggesting that the lettuce drop resistance in Eruption (indicated by low disease incidence or rating) was unrelated to bolting. The rates of bolting of DYWS and 11-G99 were statistically similar, likely because 11-G99 is photoperiod sensitive and bolts late during fall seasons in the field. PI 251246 had the most rapid rate of bolting that differed from all other genotypes, and "bolting-associated factors" may have played a role in its low DSI. In fall17, the stem strength of PI 251246 was more than

TABLE 4

Mean values of days to flowering, plant height, and basal stem diameter, and other characteristics of lettuce accessions and symptoms exhibited after inoculation with *Sclerotinia minor*[y]

Genotype × experiment[z]	Days to flowering	Plant height	Basal stem diameter	Days to mycelium emergence	Days to cortex softening	Days to collapse	Proportion collapsed	Collapse rating	Days to lower leaf discoloration	Days to leaf wilting
Eruption:gh1	149.30 d	52.62 f	12.66 d	1.07 c	2.90 cde	7.89 bc	0.17 cd	0.41 cd	3.77 ef	4.60 cd
Eruption:gh2	184.13 b	60.92 ef	11.79 d	1.13 c	2.97 cde	11.22 b	0.33 bc	0.52 bc	3.93 ef	5.47 cd
RG:gh1	123.43 e	51.10 f	9.93 e	2.00 b	4.10 b	7.93 bc	0.47 b	0.75 b	5.00 de	6.03 c
RG:gh2	163.77 cd	33.47 g	9.47 e	1.00 c	3.33 bcd	19.25 a	0.10 d	0.16 de	4.47 ef	4.50 cd
Salinas:gh1	152.33 cd	80.35 d	9.92 e	1.37 c	2.40 e	5.85 bc	0.80 a	1.18 a	3.20 f	3.40 d
Salinas:gh2	225.60 a	70.68 de	14.89 c	1.13 c	2.14 e	6.32 bc	0.51 b	0.80 b	3.43 f	4.08 cd
DYWS:gh1	132.67 e	115.84 b	21.76 a	1.14 c	2.97 cde	5.17 c	0.78 a	1.17 a	3.61 f	4.14 cd
DYWS:gh2	167.74 c	91.60 c	16.62 b	1.19 c	2.57 de	7.10 bc	0.76 a	1.20 a	3.95 ef	5.05 cd
PI251246:gh1	49.50 g	101.34 c	8.07 f	3.10 a	nd	na	0.00 d	0.00 e	7.37 b	10.63 b
PI251246:gh2	62.47 g	92.70 c	6.94 f	2.00 b	3.00 cde	na	0.00 d	0.00 e	5.97 cd	10.17 b
11-G99:gh1	106.55 f	162.53 a	7.32 f	3.26 a	7.23 a	na	0.00 d	0.00 e	9.88 a	13.36 a
11-G99:gh2	103.57 f	118.7 b	4.36 g	2.13 b	3.70 bc	na	0.00 d	0.00 e	6.93 bc	10.93 ab

[y] Different letters indicate significant differences (at $P < 0.05$) within columns for each parameter; nd = not determined and na = not applicable.
[z] Abbreviations: gh1 = greenhouse experiment 1; gh2 = greenhouse experiment 2; RG = Reine des Glaces; and DYWS = Da Ye Wo Sun.

TABLE 5

Mean values of days to shoot wilting and lesion length and related characteristics of lettuce accessions and symptomatology of lettuce drop after inoculation with *Sclerotinia minor*[y]

Genotype × experiment[z]	Days to shoot wilting	Days to mortality	Lesion length (week 1)	Lesion length (week 2)	Lesion l ength (week 3)	Lesion length (week 4)	Lesion length (week 5)	Area under lesion progress curve	Lesion length (final)	Days to evaluation for sclerotia formation
Eruption:gh1	6.17 d	8.60 f	1.87 cde	5.40 ab	6.16 de	6.20 cd	6.20 de	22.73 cd	6.20 de	37.40 bc
Eruption:gh2	7.90 c	10.60 de	1.07 ef	3.50 b	4.03 f	4.03 d	4.03 f	14.66 d	4.03 f	36.50 bcd
RG:gh1	7.70 c	9.13 ef	1.23 def	3.54 b	4.30 ef	4.30 d	4.30 ef	15.51 d	4.30 ef	33.40 e
RG:gh2	6.73 cd	11.80 d	1.34 def	4.42 ab	5.20 def	5.20 d	5.20 ef	18.75 cd	5.20 ef	35.00 cde
Salinas:gh1	4.67 e	6.60 g	2.59 bc	3.72 b	3.85 f	3.85 d	3.85 f	15.93 cd	3.85 f	27.60 f
Salinas:gh2	6.03 de	8.93 ef	1.81 cde	3.61 b	4.22 ef	4.22 d	4.22 ef	15.96 cd	4.22 ef	36.64 bcd
DYWS:gh1	5.47 de	7.44 fg	4.27 a	9.40 ab	13.62 b	14.24 a	14.30 b	48.68 a	14.30 b	33.94 de
DYWS:gh2	8.07 c	12.26 d	2.3 bcd	4.60 ab	4.91 def	4.91 d	4.91 ef	19.17 cd	4.91 ef	34.79 cde
PI 251246:gh1	nd	14.90 c	3.35 ab	12.02 a	16.42 a	16.79 a	19.11 a	47.89 a	19.11 a	34.50 cde
PI 251246:gh2	13.07 b	16.37 bc	1.36 def	6.12 ab	10.60 c	12.70 ab	12.70 bc	37.14 b	12.70 bc	36.00 bcde
11-G99:gh1	15.24 a	18.29 ab	0.38 f	2.29 b	6.57 d	9.42 bc	10.94 c	24.26 c	12.06 c	52.74 a
11-G99:gh2	15.93 a	18.87 a	1.47 def	3.71 b	5.74 def	6.71 cd	7.66 d	21.47 cd	7.66 d	38.67 b

[y] Different letters indicate significant differences (at $P < 0.05$) within columns for each parameter; nd = not determined.
[z] Abbreviations: gh1 = greenhouse experiment 1; gh2 = greenhouse experiment 2; RG = Reine des Glaces; and DYWS = Da Ye Wo Sun.

threefold (14,892 versus 4,640 g of force) and fourfold (14,892 versus 3,495 g of force) stronger than 11-G99 and Eruption, the next strongest and the weakest accessions, respectively.

Effect of plant canopy on RH and temperature, and lettuce drop in the field

In the analysis of the variations in RH and temperature, the control plots, as expected, had the highest mean temperature (in spr17) and the lowest RH (in both spr17 and fall17 experiments) (Fig. 4; Supplementary Table S2). Both RH and temperature failed to discriminate the three "treatment groups" (control, slow bolting, and rapid bolting genotypes) compared in these experiments. However, the two relatively rapid-bolting genotypes (PI 251246 and DYWS) recorded the lowest comparable RH in both experiments. The control plot in fall17 had higher RH than under the canopy of PI 251246 or DYWS, perhaps because the microsites housing the control loggers retained consistently moist conditions after continuous irrigations (or rains) coupled with seasonal low temperature; the control plots in fall17 had the lowest mean temperature. The

TABLE 6

Mean values of degradation length of the stem, height to which sclerotia formed, and additional symptoms exhibited by lettuce accessions after inoculation with *Sclerotinia minor*[y]

Genotype × experiment[z]	Cortex degradation length		Basal stem degradation length	Sclerotia height		Pith degradation height		Internal discoloration height		Root degradation severity
	Completely	Partially		Externally	Internally	Completely	Partially	Completely	Partially	
Eruption:gh1	0.00 b	0.02 d	1.09 c	0.61 de	1.60 ef	2.05 def	2.34 cd	4.41 cd	1.51 c	0.78 ab
Eruption:gh2	0.12 b	0.03 d	1.62 ab	0.13 e	2.87 de	2.67 bcd	1.32 d	3.32 def	2.36 c	0.65 bc
RG:gh1	0.00 b	0.00 d	1.67 a	0.95 cde	0.63 f	1.99 def	0.80 d	2.35 ef	1.06 c	0.53 c
RG:gh2	0.00 b	0.00 d	1.24 bc	1.43 cd	2.76 de	2.51 cde	1.69 d	3.05 ef	2.99 c	0.50 c
Salinas:gh1	0.00 b	0.00 d	0.99 c	0.62 de	1.50 ef	1.27 f	1.25 d	2.07 f	1.54 c	1.00 a
Salinas:gh2	0.00 b	0.02 d	0.18 d	0.24 e	1.63 ef	2.11 def	1.02 d	2.77 ef	3.70 bc	0.71 bc
DYWS:gh1	0.05 b	0.01 d	0.21 d	0.95 cde	1.75 ef	1.46 ef	2.5 cd	5.44 bc	4.95 bc	0.13 d
DYWS:gh2	0.02 b	0.02 d	0.20 d	0.20 e	2.72 de	1.85 def	1.75 d	3.41 de	3.68 bc	0.82 ab
PI 251246:gh1	nd	11.75 a	0.00 d	7.92 a	12.51 a	nd	26.02 a	nd	32.88 a	0.06 d
PI 251246:gh2	0.00 b	2.40 b	0.00 d	1.19 cd	7.07 b	6.03 a	5.08 b	17.04 a	4.38 bc	0.00 d
11-G99:gh1	0.67 a	0.50 c	0.02 d	1.76 bc	5.54 c	3.40 bc	4.55 bc	4.52 cd	7.96 b	0.00 d
11-G99:gh2	0.00 b	0.00 d	0.00 d	2.45 b	3.90 d	3.69 b	4.65 bc	6.67 b	4.66 bc	0.00 d

[y] Different letters indicate significant differences (at $P < 0.05$) within columns for each parameter; nd = not determined.
[z] Abbreviations: gh1 = greenhouse experiment 1; gh2 = greenhouse experiment 2; RG = Reine des Glaces; and DYWS = Da Ye Wo Sun.

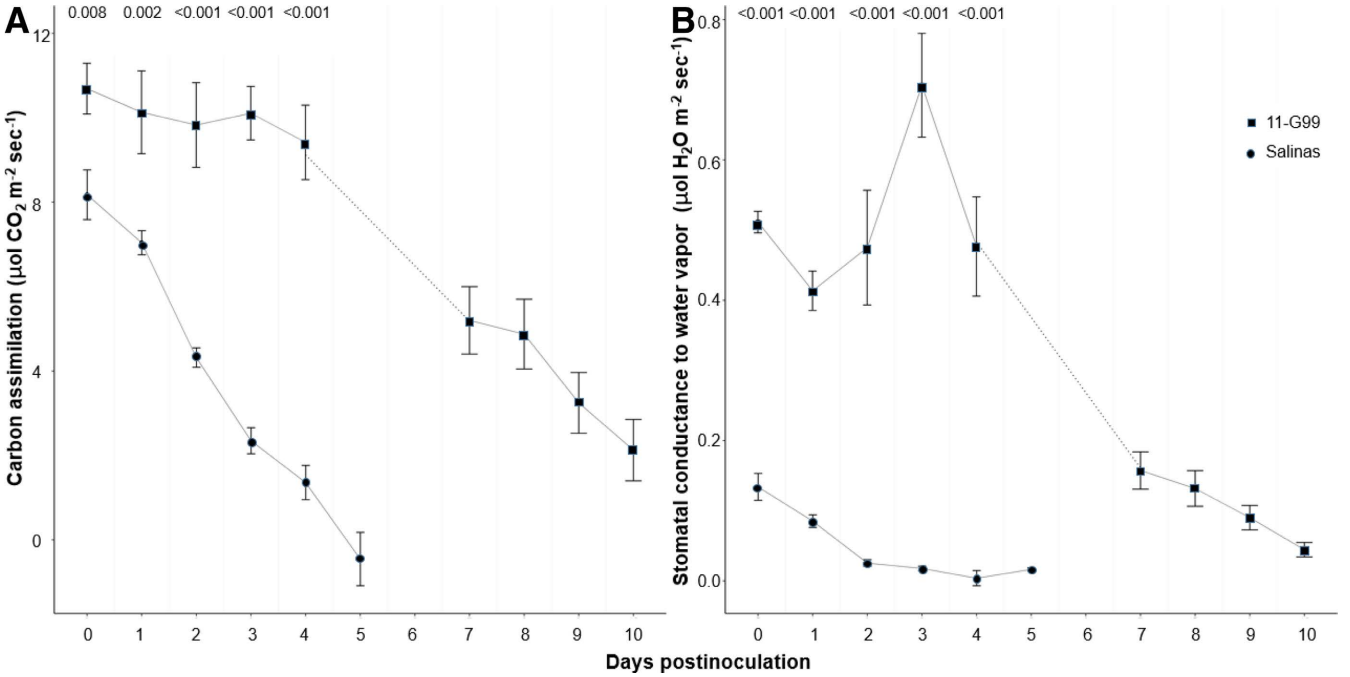

FIGURE 3
Effect of lettuce drop (*Sclerotia* spp.) on **A,** carbon assimilation (*A*) and **B,** stomatal conductance (g_s) of the selected lettuce genotypes inoculated with the pathogen in the greenhouse during experiment 2 (September 2017 to April 2018). The dotted line in each panel connects through missing data; measurements were not recorded on days 5 and 6 postinoculation in 11-G99. Error bars represent the standard error of the mean. *P* values are shown at the top of panel A. Differences in *A* between the genotypes were significant ($P \leq 0.008$) on each day measurements were taken for both samples. For g_s, significant differences were detected at $P < 0.001$ on each day measurements were taken for both genotypes.

leaf-type lettuce genotypes Eruption and RG recorded significantly higher RH under their canopies compared with PI 251246 and DYWS, respectively. Salinas, the head-type genotype, and the *L. serriola* accession 11-G99 had inconsistent RH measurements; Salinas (fall17) and 11-G99 (spr17) had equal RH. During fall17, 11-G99 had a relatively higher RH that was closer to that of RG, as expected. Due to its photoperiodic sensitivity, 11-G99 exhibits a prostrate growth habit during fall seasons. The rosette leaf canopy may have contributed to the retention of higher RH by the accession in fall17. The different lettuce types did not show noticeable variations concerning temperature under their canopies in both experiments, indicating that temperature is not a major factor in differentiating the outcome of the interaction between *Sclerotinia* spp. and lettuce genotypes with different growth architectures.

Correlations between lettuce drop symptomatology and plant architecture

In experiment gh1, height to which sclerotia formed aboveground (internally) was positively correlated with xylem (r = 0.77, P = 0.0002) and pith strengths (r = 0.73, P = 0.0006), days to mycelium emergence (r = 0.71, P = 0.0011), days to lower leaf discoloration (r = 0.63, P = 0.0047) and leaf wilting (r = 0.68, P = 0.002), days to mortality (r = 0.66, P = 0.0027), lesion lengths (weeks 2 to final) (r = 0.60 to 0.79, P = 0.0091 to 0.0001), area under the lesion progress curve (r = 56, P = 0.0162), and height to which sclerotia formed aboveground externally (r = 0.95, P = 2.76e–09). It was negatively correlated with days to flowering (r = –0.92, P = 5.70e-08), collapse rating (r = –0.66, P = 0.0029), basal stem degradation length (r = –0.63, P = 0.005), and root degradation severity (r = –0.55, P < 0.0178) (Supplementary Fig. S2; Supplementary Table S3). Similar trends in correlations were observed in gh2 (Supplementary Fig. S3; Supplementary Table S4). Most of the individual variables were positively correlated between the two experiments (Fig. 5; Supplementary Table S5). A negative correlation was detected between the experiments for a few of the variables (e.g., the final lesion lengths: ID2 and 54), perhaps due to the influence of weather variations.

Correlation of physiological traits (photosynthetic gas exchange and chlorophyll fluorescence) and symptomatology of lettuce drop in 11-G99

Correlation data were evaluated on a leaf-by-leaf basis in 11-G99 during the late stage of infection because values of traits

TABLE 7

Mean values of stem mechanical strength (cortex, xylem, and pith) and basal stem diameter of lettuce accessions grown in the greenhouse and field and evaluated for their reaction to *Sclerotinia minor*[y]

Genotype × experiment[z]	Cortex strength (g of force)	Xylem tissue strength (g of force)	Pith tissue strength (g of force)	Stem diameter (mm)
Eruption:gh1	2,251.50 bc	3,480.06 cd	1,718.33 cde	14.06 hi
Eruption:gh2	2,371.76 abc	4,131.59 c	2,011.22 c	13.76 i
Eruption:fall17	1,053.78 e	1,482.32 f	959.11 ef	24.24 c
RG:gh1	2,121.62 c	2,654.16 cdef	1,738.15 cd	16.66 fg
RG:gh2	2,086.99 cd	2,651.74 cdef	1,609.33 cdef	16.88 ef
RG:fall17	1,112.09 e	1,437.50 f	1,008.54 def	32.78 b
Salinas:gh1	2,290.85 bc	3,013.40 cdef	1,643.78 cdef	18.47 d
Salinas:gh2	2,417.12 abc	3,024.58 cdef	1,766.71 cd	18.22 de
Salinas:fall17	1,425.58 e	1,565.47 ef	930.68 f	24.48 c
Da Ye Wo Sun:gh1	2,575.41 abc	3,338.38 cde	1,688.91 cdef	15.5 fg
Da Ye Wo Sun:gh2	2,470.57 abc	3,918.25 c	1,893.20 c	15.27 gh
Da Ye Wo Sun:fall17	1,564.34 de	1,658.39 ef	961.52 ef	34.46 a
PI 251246:gh1	2,360.67 abc	8,790.47 a	5,021.83 a	9.50 j
PI 251246:gh2	2,437.62 abc	8,180.30 ab	4,914.08 a	9.92 j
PI 251246:fall17	2,439.78 abc	8,363.38 ab	4,088.49 b	25.05 c
11-G99:gh1	2,848.67 a	7,471.15 ab	4,898.49 a	7.15 k
11-G99:gh2	2,706.11 ab	6,602.76 b	3,845.06 b	7.44 k
11-G99:fall17	1,107.33 e	2,075.94 def	1,457.01 cdef	15.57 fg

[y] Different letters indicate significant differences (at P < 0.05) within columns for each parameter.
[z] Abbreviations: gh1 = greenhouse experiment 1; gh2 = greenhouse experiment 2; fall17 = fall 2017 field experiment; and RG = Reine des Glaces.

TABLE 8

Mean values of lettuce drop disease incidence (DI), disease rating, standardized area under the disease progress stairs (sAUDPS), sAUDPS residual, disease severity index (DSI), and rate of bolting of lettuce accessions evaluated in the field[y]

Genotype	DI	Disease rating	sAUDPS	sAUDPS residual	DSI[z]	Bolting rate
Eruption	0.20 d	0.28 d	0.09 de	−0.13 ef	83.34 bc	1.29 d
Reine des Glaces	0.68 ab	0.91 ab	0.40 a	0.14 ab	93.80 ab	1.00 d
Salinas	0.50 bc	0.68 abc	0.19 cd	−0.06 def	91.11 ab	1.00 d
Da Ye Wo Sun	0.35 bcd	0.61 abcd	0.15 cde	−0.01 bcde	93.33 ab	3.75 bc
PI 251246	0.16 d	0.27 d	0.05 de	−0.04 cde	41.49 d	6.33 a
11-G99	0.27 cd	0.40 cd	0.11 de	−0.04 cde	100.00 a	2.58 c
Brave Heart	0.47 bcd	0.65 abc	0.19 bcd	−0.06 def	nd	1.00 d
Green Forest	0.54 bc	0.72 abc	0.25 bc	0.02 bcd	nd	1.21 d
Hearts Delight	0.69 ab	0.92 a	0.31 ab	0.05 bc	71.43 c	1.13 d

[y] Different letters indicate significant differences (at P < 0.05) within columns for each parameter; nd = not determined.
[z] The DSI presented is calculated from a measurement conducted in the fall 2017 field experiment. For the rest of the variables, the values are from a two-way analysis of variance from data of four lettuce drop experiments (i.e., spring 2016, spring 2017, fall 2016, and fall 2017).

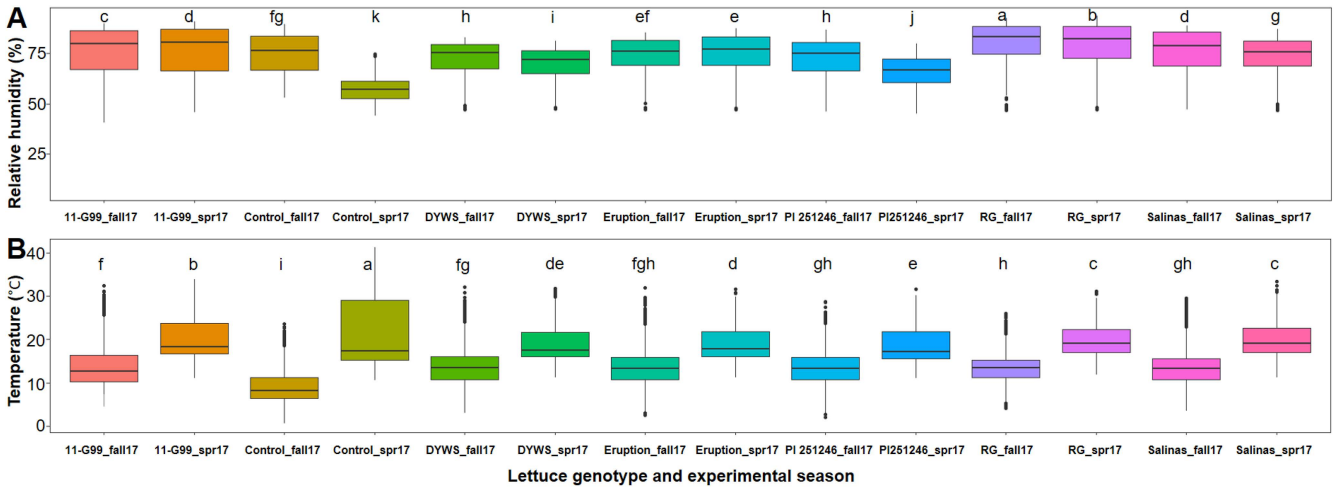

FIGURE 4

Boxplots depicting the effects of lettuce genotypes on **A,** relative humidity (%) and **B,** temperature (°C) under host plant canopy measured in lettuce drop field experiments in Salinas Valley, CA in spring and fall seasons in 2017 (spr17 and fall17). Evaluations were made under the leaf canopy of the genotypes 11-G99, Da Ye Wo Sun (DYWS), Eruption, PI 251246, Reine des Glaces (RG), and Salinas. Controls are data values measured at microsites without any plant. Five statistics (bars) are represented in each boxplot from bottom to top: the smallest observation, lower quartile, median, upper quartile, and largest observation. Data points positioned outside this range and depicted as black circles are outliers. Global differences among the treatments were significant ($P \leq$ 2.2e-16) for both relative humidity and temperature. Different letters on top of the bars indicate significant differences among the means within plots for each parameter (Tukey-Kramer honestly significant difference test, $P < 0.05$) (Tukey 1949).

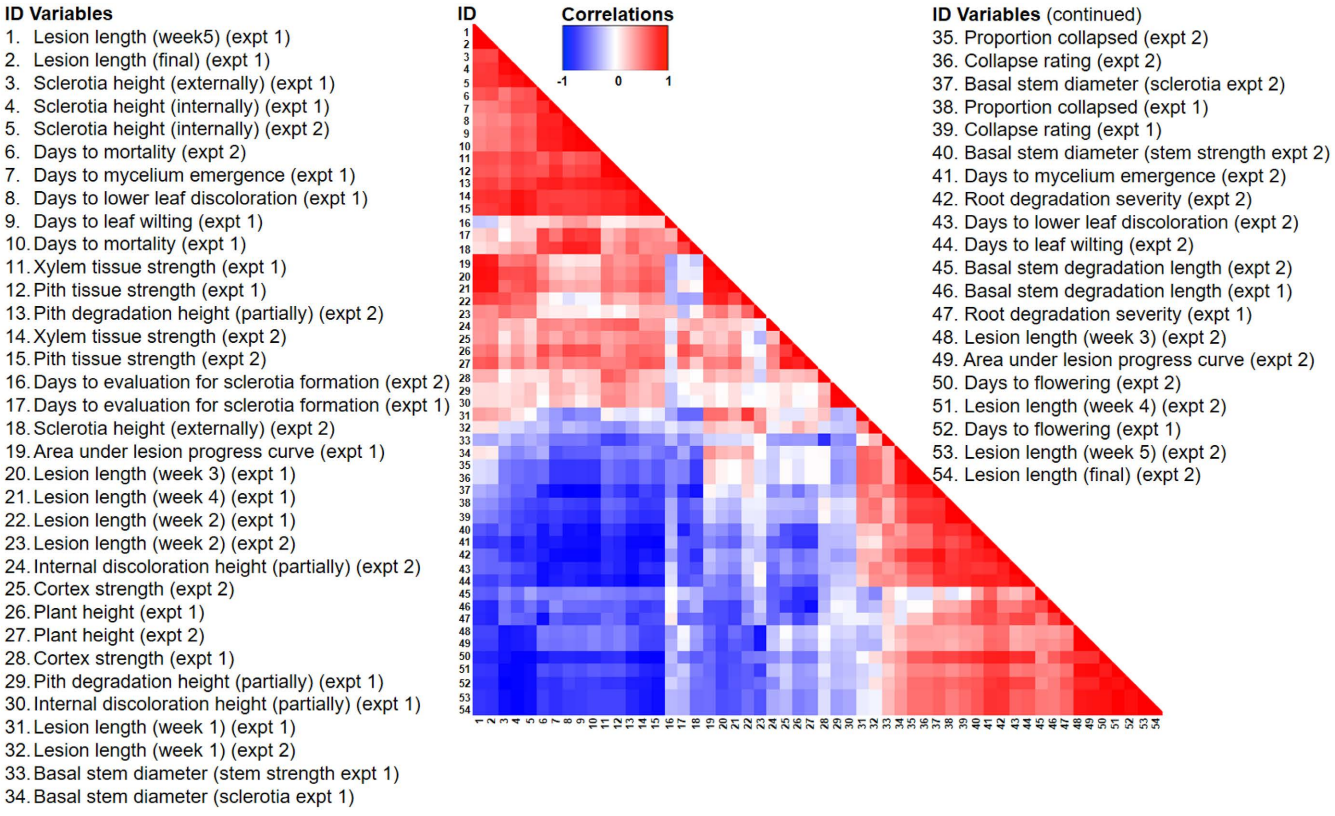

FIGURE 5

Heatmap (hierarchical cluster) of Pearson correlation (*r*) matrix for days to flowering, plant height, basal stem diameter, basal stem (cortex, xylem, and pith) strength, and aboveground signs or symptoms of lettuce drop and sclerotia formation aboveground of lettuce genotypes after inoculation with *Sclerotinia minor* (greenhouse experiments [Expt] 1 and 2). The scale for *r* is indicated in a color bar at the top center. See Supplementary Table S5 for details.

tended to decline faster in lower leaves than in the upper leaves. *A* had a strong positive correlation with stomatal conductance ($r = 0.82$, $P < 0.001$) and chlorophyll concentration ($r = 0.70$, $P < 0.001$) in every leaf, as expected in a healthy plant. *A* in the lower leaf was positively correlated with days to mycelium growth ($r = 0.71$, $P < 0.001$), days to lower leaf discoloration ($r = 0.60$, $P < 0.001$), and days to basal stem softening ($r = 0.41$, $P = 0.009$). Chlorophyll concentration of the lower leaves correlated with days to lower leaf discoloration ($r = 0.66$, $P < 0.001$), days to mycelium growth ($r = 0.44$, $P = 0.003$), and days to wilting of leaves ($r = 0.45$, $P = 0.005$). A decline in (leaf) chlorophyll concentration and lower-leaf discoloration are the same phenotypic attributes reflecting severe plant infection. *A* in the upper leaves was positively correlated with days to leaf wilting ($r = 0.63$, $P < 0.001$), days to mycelium growth ($r = 0.044$, $P = 0.005$), days to mortality ($r = 0.60$, $P < 0.001$), and plant height (see above). *qP* in the upper leaves was correlated with days to lower leaf discoloration ($r = 0.35$, $P = 0.03$), days to leaf wilting ($r = 0.45$, $P = 0.004$), and days to mortality ($r = 0.36$, $P = 0.02$). *qP* in the lower leaves was correlated with days to basal stem softening ($r = 0.42$, $P = 0.01$), days to lower leaf discoloration ($r = 35$, $P = 0.03$), and days to leaf wilting ($r = 0.34$, $P = 0.04$).

Correlation of microclimate conditions under plant canopy and lettuce drop in the field

Strong positive correlation was detected between RH and lettuce drop incidence-derived variables ($r = 0.43$ to 0.49, $P = 5.48e\text{-}09$ to $5.04e\text{-}07$) in spr17; temperature was not significantly correlated with disease during this season ($r = 0.02$ to 0.04, $P = 0.64$ to 0.83). A weak negative correlation ($r = –0.46$, $P = 0.0549$) was observed between RH and bolting in spr17 when the data at harvest maturity were analyzed.

In fall17, lettuce drop was significantly positively correlated with RH and negatively correlated with temperature (Table 9). Disease incidence was lower at lower RH and higher temperature, and higher at higher RH and lower temperature (Fig. 6). The lack of correlation between temperature and disease incidence in spr17 is likely due to the relatively higher temperature (ranging between 17.11 and 22.38°C) that failed to influence disease development in a statistically trackable fashion. The mean weekly temperature ranged between 10.76 and 17.91°C during the fall17 season.

To increase the statistical power of the analysis, we combined the weekly mean datasets of the spr17 and fall17 seasons and computed correlations between disease and microclimate variables. The result confirmed the significant positive correlation between RH and disease incidence or rating ($r = 0.42$ to 0.49, $P = 9.30e\text{-}11$ to $5.76e\text{-}15$). Again, no association was detected between disease and temperature ($r = –0.03$ to 0.05, $P = 0.5028$ to 0.6124).

The rate of bolting was evaluated only toward the end of the experiment in spr17; thus, the variable was not included in the preceding analysis. Using the combined weekly mean datasets of the spr17 and fall17 experiments but retaining only materials with complete values for all the variables, including the rate of bolting, indicated a positive correlation between bolting and temperature ($r = 0.34$; $P = 2.01e\text{-}04$). Disease rating or incidence was positively correlated ($r = 0.54$ to 0.45, $P = 8.28e\text{-}10$ to $2.62e\text{-}07$) with humidity. Bolting was not correlated with disease ($r = 0.09$ to 0.12, $P = 0.1971$ to 0.3403) or RH ($r = –0.06$, $P = 0.5531$).

Correlation of lettuce drop, basal stem mechanical strength, bolting, and microclimate conditions in the field

We also conducted correlation analysis using the mean data for lettuce drop, basal stem strength, basal stem diameter, bolting score, and microclimate conditions in fall17, when measurements for all these variables were collected. DSI was significantly negatively associated with basal stem strength ($r = –0.92$, $P = 3.48e\text{-}07$ for xylem strength) and bolting ($r = –0.88$, $P = 5.46e\text{-}06$) (Table 10). The standardized area under the disease progress stairs and disease incidence were positively correlated with RH ($r = 0.58$ and 0.51, $P = 0.02$ and 0.04, respectively) but DSI was not ($r = 0.33$, $P = 0.2157$). Basal stem strength (cortex, xylem, and pith components) and bolting had strong positive associations ($r = 0.70$ to 0.91, $P = 0.0027$ to $9.32e\text{-}07$). Finally, we analyzed correlation of variables between the spr17 and fall17 field experiments. The result confirmed the consistency of positive correlations ($r = 0.48$ to 0.67, $P = 7.36e\text{-}14$ to $7.40e\text{-}07$) between lettuce drop incidence or rating and RH; only temperature from the fall experiment was negatively correlated ($r = –0.54$ to $–0.27$, $P = 1.652e\text{-}08$ to 0.0076) with lettuce drop datasets from both experiments (Table 11). The temperature in spr17 experiment was negatively associated ($r = –0.39$, $P = 7.44e\text{-}05$) with the bolting

TABLE 9

Pearson correlation coefficients for lettuce drop disease incidence (DI), disease rating (DR), bolting rate (BR), relative humidity (RH), and temperature (Temp) in the six lettuce genotypes evaluated in the field in Salinas Valley, CA in fall 2017[z]

Trait	DI	DR	BR	RH	Temp
DI	–	0.95	0.05	0.64	−0.47
DR	<2.2e-16	–	0.05	0.67	−0.54
BR	0.6319	0.5958	–	−0.05	−0.15
RH	1.823e-12	7.361e-14	0.6249	–	−0.57
Temp	0.0000	1.652e-08	0.1425	1.15e-09	–

[z] Correlation coefficients are shown above the self-correlations (– indicates perfect or self-correlation). Given at the bottom half are the corresponding *P* values. Results were generated from the weekly average disease, bolting score, and microclimate conditions data from disease onset to harvest maturity (20 October to 1 December 2017).

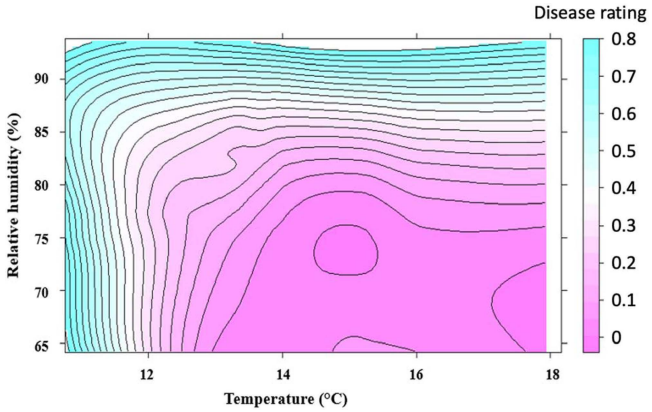

FIGURE 6

Plot depicting the relationship of lettuce drop (*Sclerotinia minor*) disease rating (of all genotypes) with average temperature and relative humidity (RH). This graph was produced from the weekly average microclimate conditions and disease incidence from the lettuce drop field experiment in Salinas, CA in fall 2017 (from disease onset to harvest maturity; 20 October to 1 December 2017). The plot indicates the level of disease incidence based on the temperature and the RH (lowest incidence shown at lower right corner when temperature was high and humidity low).

TABLE 10

Pearson correlation coefficients for lettuce drop disease incidence (DI), disease rating (DR), standardized area under the disease progress stairs (sAUDPS), sAUDPS residual (sR), disease severity index (DSI), cortex strength (CS), xylem strength (XS), pith strength (PS), basal stem diameter (SD), bolting rate (BR), relative humidity (RH), and temperature (Temp) in the six lettuce genotypes evaluated in the field in Salinas Valley, CA in fall 2017[z]

Trait	DI	DR	sAUDPS	sR	DSI	CS	XS	PS	SD	BR	RH	Temp
DI	–	0.99	0.95	0.91	0.31	−0.32	−0.18	−0.12	0.05	−0.18	0.51	−0.38
DR	1.303e-13	–	0.92	0.88	0.29	−0.29	−0.16	−0.10	0.07	−0.16	0.46	−0.41
sAUDPS	2.86e-08	6.23e-07	–	0.97	0.29	−0.32	−0.23	−0.18	0.13	−0.15	0.58	−0.25
sR	1.07e-06	5.43e-06	6.42e-10	–	0.10	−0.18	−0.03	0.01	0.14	0.09	0.45	−0.26
DSI	0.2503	0.2714	0.268	0.7161	–	−0.62	−0.92	−0.90	0.01	−0.88	0.33	−0.04
CS	0.2279	0.2727	0.382	0.5146	1.04e-02	–	0.72	0.62	−0.08	0.70	−0.23	0.28
XS	0.4959	0.5445	0.382	0.9011	3.48e-07	0.0018	–	0.99	−0.06	0.91	−0.28	0.06
PS	0.6603	0.7228	0.4956	0.962	1.53e-06	0.0108	2.10e-12	–	−0.06	0.89	−0.27	−0.01
SD	0.8525	0.7832	0.6361	0.6076	0.9645	0.7664	0.8246	0.8351	–	0.04	−0.02	0.13
BR	0.5016	0.5422	0.5858	0.738	5.46e-06	0.0026	9.32e-07	4.15e-06	0.8804	–	−0.39	0.08
RH	0.0434	0.0763	0.0183	0.0796	0.2157	0.3819	0.287	0.3168	0.9284	0.1302	–	0.16
T	0.1518	0.1125	0.3465	0.3233	0.8863	0.2996	0.8187	0.9793	0.6393	0.7684	0.548	–

[z] Correlation coefficients are shown above the self-correlations (– indicates perfect or self-correlation). Given at the bottom half are the corresponding *P* values. Results were generated from the mean values of disease, stem mechanical strength, bolting score, and microclimate conditions data. Stem mechanical strength and diameter were measured at harvest maturity.

TABLE 11

Pearson correlation coefficients for lettuce drop disease incidence (DI), disease rating (DR), relative humidity (RH), temperature (Temp), and bolting rate (BR) in the six lettuce genotypes evaluated in the field in Salinas Valley, CA in spring and fall 2017[z]

Trait	DI_1	DI_2	DR_1	DR_2	RH_1	RH_2	$Temp_1$	$Temp_2$	BR_2
DI_{spr}	–	0.60	0.96	0.57	0.51	0.51	0.06	−0.27	0.03
DI_{fall}	7.39e-11	–	0.55	0.95	0.48	0.64	0.06	−0.47	0.05
DR_{spr}	<2.2e-16	4.92e-09	–	0.54	0.57	0.54	0.03	−0.31	0.01
DR_{fall}	1.40e-09	<2.2e-16	9.77e-09	–	0.53	0.67	0.01	−0.54	0.05
RH_{spr}	1.23e-07	7.40e-07	1.90e-09	2.02e-08	–	0.77	−0.22	−0.61	−0.08
RH_{fall}	1.23e-07	1.82e-12	1.54e-08	7.36e-14	<2.2e-16	–	−0.15	−0.57	−0.05
T_{spr}	0.5539	0.5686	0.8088	0.952	0.0313	0.1446	–	0.55	−0.39
T_{fall}	0.0076	1.04e-06	0.0024	1.652e-08	3.15e-11	1.15e-09	7.65e-09	–	−0.15
BR_{fall}	0.7508	0.6319	0.934	0.5958	0.4112	0.6249	7.44e-05	0.1425	–

[z] Subscripts next to the trait abbreviations indicate the experimental seasons: spr = spring experiment and fall = fall experiment. Correlation coefficients are shown above the self-correlations (– indicates perfect or self-correlation). Given at the bottom half are the corresponding *P* values. Results were generated from the mean weekly values of the variables from disease onset to harvest maturity. Rate of bolting was evaluated weekly only during the fall experiment.

TABLE 12

Pearson correlation coefficients between four host plant characteristics and eight signs or symptoms of lettuce drop (*Sclerotinia* spp.) observed on the root, basal stem, cortex, pith, and whole plant on six lettuce genotypes evaluated in Salinas, CA during two consecutive greenhouse seasons (2017 to 2018)[z]

Parameters	Days to flowering (exp 1)	Days to flowering (exp 2)	Plant height (exp 1)	Plant height (exp 2)	Stem diameter (exp 1)	Stem diameter (exp 2)	Xylem tissue strength (exp 1)	Xylem tissue strength (exp 2)
Collapse rating (exp 1)	0.64**	0.78***	–0.32	–0.34	0.60**	0.83***	–0.58*	–0.77***
Collapse rating (exp 2)	0.58*	0.64**	–0.08	0.04	0.87***	0.87***	–0.50*	–0.52*
Days to mortality (exp 1)	–0.69**	–0.81***	0.68**	0.55*	–0.58*	–0.93***	0.70**	0.79***
Days to mortality (exp 2)	–0.74***	–0.85***	0.71***	0.58*	–0.28	–0.80***	0.62**	0.77***
Basal stem degradation length (exp 1)	0.53*	0.63**	–0.77***	–0.89***	–0.06	0.33	–0.57*	–0.72***
Base stem degradation length (exp 2)	0.46	0.43	–0.78***	–0.76***	0.04	0.20	–0.45	–0.50*
Sclerotia height (externally) (exp 1)	–0.94***	–0.87***	0.22	0.33	–0.35	–0.44	0.66**	0.80***
Sclerotia height (externally) (exp 2)	–0.50*	–0.59**	0.57*	0.22	–0.58*	–0.87***	0.34	0.44
Sclerotia height (internally) (exp 1)	–0.92***	–0.92***	0.41	0.52*	–0.43	–0.57*	0.77***	0.93***
Sclerotia height (internally) (exp 2)	–0.89***	–0.92***	0.28	0.36	–0.36	–0.56*	0.73***	0.88***
Pith degradation height (partially) (exp 1)	–0.23	–0.23	0.05	0.03	–0.32	–0.28	0.43	0.25
Pith degradation height (partially) (exp 2)	–0.83***	–0.88***	0.61**	0.60**	–0.45	–0.80***	0.91***	0.89***
Internal discoloration height (partially) (exp 1)	–0.20	–0.19	0.01	0.05	–0.30	–0.23	0.47*	0.26
Internal discoloration height (partially) (exp 2)	–0.41	–0.41	0.52*	0.48*	–0.16	–0.38	0.58*	0.4
Root degradation severity (exp 1)	0.67**	0.76***	–0.68**	–0.58*	–0.05	0.52*	–0.51*	–0.65**
Root degradation severity (exp 2)	0.82***	0.89***	–0.53*	–0.45	0.68**	0.93***	–0.77***	–0.84***

[z] Abbreviations: exp 1 = greenhouse experiment 1 and exp 2 = greenhouse experiment 2. Asterisks ***, **, and * indicate $P < 0.001$, 0.01, and 0.05, respectively. The rest are not significant at $P < 0.05$.

TABLE 13

Linear models obtained through stepwise and best-subset regression analyses for predicting lettuce drop (*Sclerotinia* spp.) in the greenhouse and field from days to flowering (DTF), plant height (PH), basal stem diameter (SD), xylem strength (XS), and bolting rate (BR) of lettuce genotypes, and relative humidity (RH) and temperature (Temp) under the host plant canopy

Response variable	Predictor variable[t]	Exp[u]	N[v]	Specific predictor	P value	R^{2w}	Models[x]	P value[y]	R^2_{adj}[z]
Collapse rating (CR)	Agromorphological and stem mechanical strength traits	gh1	18	DTF	0.0040	0.41	CR = −0.7929 + 0.0073 × DTF + 0.0442 × SD	0.0023	0.50
			18	SD	0.0087	0.36			
			18	XS	0.0123	0.33			
		gh2	18	SD	1.71e-05	0.70	CR = −3.363 + 3.122 × SD − 9.771e-05 × XS	1.637e-05	0.74
			18	XS	0.0002	0.59			
			18	DTF	0.0002	0.60			
Days to mortality (DTM)	Agromorphological and stem mechanical strength traits	gh1	18	SD	2.00e-08	0.87	DTM = 58.1517 − 35.5930 × SD + 0.0317 × PH	3.048e-09	0.92
			18	PH	0.0021	0.46			
			18	XS	0.0012	0.49			
			18	DTF	0.0014	0.48			
		gh2	18	SD	5.07e-06	0.74	DTM = 1.8273 − 0.0077 × SD − 0.072180 × DTF	4.733e-06	0.78
			18	DTF	0.0014	0.48			
			18	PH	0.0021	0.46			
			18	XS	0.0012	0.49			
Basal stem degradation length (BsDL)	Agromorphological and stem mechanical strength traits	gh1	18	PH	0.0002	0.60	BsDL = 1.9225 − 0.0134 × PH	−	−
			18	XS	0.0142	0.32			
			18	DTF	0.023	0.28			
		gh2	18	PH	0.0003	0.57	BsDL = 4.1403 − 0.7873 × PH	−	−
			18	XS	0.0346	0.25			
Sclerotia height (externally; SH_{ext})	Agromorphological and stem mechanical strength traits	gh1	18	DTF	1.12e-08	0.88	SH_{ext} = 10.6518 − 0.0716 × DTF	−	−
			18	XS	0.0029	0.43			
		gh2	18	SD	2.39e-06	0.76	SH_{ext} = 12.131 − 7.911 × SD	−	−
			18	DTF	0.0098	0.35			
Sclerotia height (internally; SH_{int})	Agromorphological and stem mechanical strength traits	gh1	18	DTF	5.70e-08	0.85	SH_{int} = 17.15312 − 0.1112 × DTF	−	−
			18	XS	0.0002	0.59			
		gh2	18	DTF	1.00e-07	0.84	SH_{int} = 19.646 − 0.1112 × DTF	−	−
			18	XS	1.49e-06	0.77			
		gh2	18	XS	8.48e-07	0.79	PDH_{par} = 9.0874 + 0.0005 × XS − 6.4372 × SD	3.914e-07	0.84
			18	SD	6.42e-05	0.64			
			18	PH	0.0090	0.36			
Internal discoloration height (partially; IDH_{par})	Agromorphological and stem mechanical strength traits	gh1	18	XS	0.0498	0.22	IDH_{par} = −0.3748 + 0.0022 × XS	−	−
		gh2	18	PH	0.0424	0.23	IDH_{par} = −0.6044 + 0.9262 × PH	−	−

(*Continued on next page*)

[t] Predictors in greenhouse experiments were days to flowering, plant height, basal stem diameter, and xylem strength. In the field experiments, relative humidity, temperature, bolting rate, basal stem diameter, and xylem strength were the predictor variables.
[u] Abbreviations: gh1 = greenhouse experiment 1; gh2 = greenhouse experiment 2; and spr17 and fall17 = spring and fall 2017 field experiments, respectively.
[v] Sample size.
[w] Coefficient of determination for univariate models
[x] The specific model was selected based on the F test or the likelihood-ratio test, the Bayesian information criterion statistic, the MALO-CP statistic, or the adjusted coefficient of determination (R^2) values.
[y] The P value for the model provided as the best representative of the data; − indicates not applicable.
[z] Adjusted coefficient of determination for multivariate models provided in the models' column; − indicates not applicable.

TABLE 13
(*Continued from previous page*)

Response variable	Predictor variable[t]	Exp[u]	N[v]	Specific predictor	P value	R^{2w}	Models[x]	P value[y]	R^2_{adj}[z]
Root degradation severity (RDS)	Agromorphological and stem mechanical strength traits	gh1	18	PH	0.0018	0.46	RDS = 0.2297 − 0.0052 × PH + 0.0057 × DTF	2.46e-04	0.63
			18	DTF	0.0022	0.45			
			18	XS	0.0294	0.26			
		gh2	18	SD	2.98e-08	0.86	RDS = −3.8059 + 1.9888 × SD + 0.4101 × DTF	8.514e-11	0.95
			18	DTF	6.43e-07	0.80			
			18	XS	1.28e-05	0.71			
Disease rating or disease severity index (DR or DSI)	Microclimate conditions, stem mechanical strength and agromorphological traits	spr17	126	RH	5.48e-09	0.24	DR = −0.6690 + 0.0126 × RH	5.48e-09	−
		fall17	16	XS	3.48e-07	0.84	DSI = 101.40 − 0.0061 × XS	3.48e-07	−
				BR	5.46e-06	0.78			
		fall17	96	RH	7.36e-14	0.45	DR = −0.6680 + 0.0170 × RH − 0.0338 × T	2.354e-13	0.47
				Temp	1.65e-08	0.29			

score in fall17. Both lettuce drop and RH were not correlated with bolting (r = –0.08 to 0.05; P = 0.4112 to 0.934).

Predicting resistance to *Sclerotinia* spp. in lettuce

Greenhouse experiments. The four explanatory variables (days to flowering, plant height, basal stem diameter, and xylem strength) were, in most cases, highly correlated with the response variables during both gh1 and gh2 experiments (Table 12). The effects of these explanatory variables on lettuce drop varied by response parameter and season. Days to flowering alone or as a component of multivariate models predicted several response variables in gh1 or gh2 (Table 13; Fig. 7). It explained 84 to 88% of the variation in height to which sclerotia formed inside the pith and outside of the cortex in the gh1 experiment or during both experiments. As components of bivariate models, days to flowering together with basal stem diameter explained 50 to 95% of the variations in response variables in gh1 or gh2. Plant height alone explained 57 to 60% of the variation in basal stem degradation length in both experiments. Plant height (along with stem diameter and days to flowering) explained 63 and 92% of the variation in days to morality and root degradation severity, respectively, during gh1. Basal stem diameter and xylem strength explained 70 and 71% of the variation in collapse rating and root degradation severity, respectively, in gh2.

Field experiments. RH explained 24% of the variation in disease rating during spr17 (Table 13; Fig. 7). A univariate model with xylem strength contributed to 84% of the variation in DSI. A bivariate model with RH and temperature explained 47% of the variation in disease rating using a separate dataset.

DISCUSSION

To our knowledge, this report is the first and by far the most comprehensive collection of data related to the epidemiology of lettuce drop and factors that influence infection responses and host resistance for diseases caused by *Sclerotinia* spp. The observation of *S. minor* sclerotia in the stem of *Lactuca* plants and characterization of its epidemiological implications as it relates to host phenology advance the knowledge of the essential role of host tissues as predisposing factors in *Sclerotinia* pathogenesis. The inherent characteristics of a host genotype determine the outcome of its interaction with *S. minor*. We observed different outcomes of infection between modern and landrace or wild ancestral genotypes, with modern cultivars being more susceptible to infection. Genotypes that tolerate lettuce drop tend to resist degradation by the pathogen. We identified basal stem mechanical strength as a strong host susceptibility or resistance factor to lettuce drop. Lettuce genotypes with development-associated lettuce drop resistance possess "disease avoidance phenotypes" (Grube 2004; Hayes et al. 2010) and have strong stems (this work). Further genetic studies indicate that resistance and stem strength appear to be linked or pleiotropic (unpublished data). In this study, we term this phenomenon "plant architecture- or stem strength-mediated resistance" (PAMR).

Previously, it was assumed that *S. minor* causes lettuce drop by infecting plant roots (Adams and Tate 1975; Dillard and Grogan 1985; Leach and Gilbert 1926; Melzer and Boland 1994) (https://www.apsnet.org/) and, aboveground, it only infects the stems and leaves in contact with the soil (Imolehin et al. 1980; Koike et al. 1997; Patterson and Grogan 1985; Subbarao et al. 1996; Wu and Subbarao 2003) (http://ipm.ucanr.edu). However, in the current study, *S. minor*-infected PI 251246 and other genotypes that produced sclerotia in their stems were standing intact without collapsing and showed no degradation on roots. We found sclerotia both inside the pith and stem cavities and outside the cortex of plants firmly standing in upright positions. This infection system appears to be analogous to Sclerotinia stem rot in rapeseed (*Brassica napus*) (Lane et al. 2019; Purdy 1979; Tziros et al. 2008).

In sunflower, direct penetration of *S. sclerotiorum* hyphae and complete colonization by mycelium through the cuticle in the basal stem of a susceptible genotype occur within 12 and

48 hpi, respectively, leading to the death of the tissue (Davar et al. 2012). In cultivated *L. sativa*, *Sclerotinia* spp. colonize the entire basal stem tissue within a short period. In the current study, the first sign of the pathogen, white fluffy mycelia (Bolton et al. 2006), emerged at the basal stem within 24 hpi (in susceptible genotypes) and 72 hpi (in the tolerant genotypes); the difference between the two groups was significant. The formation of water-soaked lesions at the basal stem, the first symptom of infection, was followed by wilting of leaves 48 to 96 and 72 to 168 hpi in susceptible and tolerant genotypes, respectively. The disease then spread to the whole plant, causing susceptible genotypes to shrivel, wilt, collapse, and die within a few days, with tolerant genotypes showing these symptoms significantly delayed or with significantly lower proportions (Supplementary Text S1) (Subbarao 1998).

Our study identified basal stem mechanical strength as a major feature of resistance or susceptibility to *S. minor* in *Lactuca* spp. This has key implications for pathogen penetration and inoculum production. Mechanically strong host tissues may create a barrier for fungal multiplication and impede successful establishment in the host. First, host plants with strong basal stem walls (resistant genotypes) may not have readily available or easily released specific physical or chemical cues required by *Sclerotinia* spp. for appressorium formation and subsequent infection. This may prevent the pathogen from triggering signal transduction pathways involved in infection-related morphogenesis and virulence or pathogenicity (Deising et al. 2000) as rapidly as in the susceptible genotypes. Tissues in resistant genotypes may also inhibit or delay the synthesis of chitin synthase, the key enzyme in chitin formation, and suppress appressoria formation or weaken its integrity and prevent pathogen entry or arrest its growth or infection processes (Garg et al. 2010; Li et al. 2016). For instance, it took only 24 hpi for actively growing mycelium to emerge at the basal stem of susceptible genotypes but 72 hpi in the tolerant ones. Genotypes with softer xylem also had shorter pith degradation heights compared with those with stronger xylem (PI 251246 and 11-G99; Supplementary Text S2).

This study is the first to measure the pathophysiological responses of resistance and susceptibility to lettuce drop under active infection, in situ, by *S. minor* in *Lactuca* spp. and correlate them with symptomatology. *A*, *qP*, stomatal conductance, and chlorophyll concentration were strongly correlated with each other and with symptomatology. The strong correlation between *A* and stomatal conductance suggests that stomatal limitations define the former even under disease pressure (Supplementary Text S3). Photosynthetic rate and stomatal conductance were higher in upper leaves, as expected, due to leaf age (Field and Mooney 1983). At the early stage of infection (1 to 3 dpi), both tolerant (11-G99) and susceptible (Salinas) genotypes exhibited a similar pattern of a spike in stomatal conductance, indicating that the difference between the two groups in reaction to the pathogen likely occurs at later stages of infection. The pathogen perhaps easily suppresses defense reactions in Salinas but faces resistance in 11-G99 until after a few more days, in agreement with the

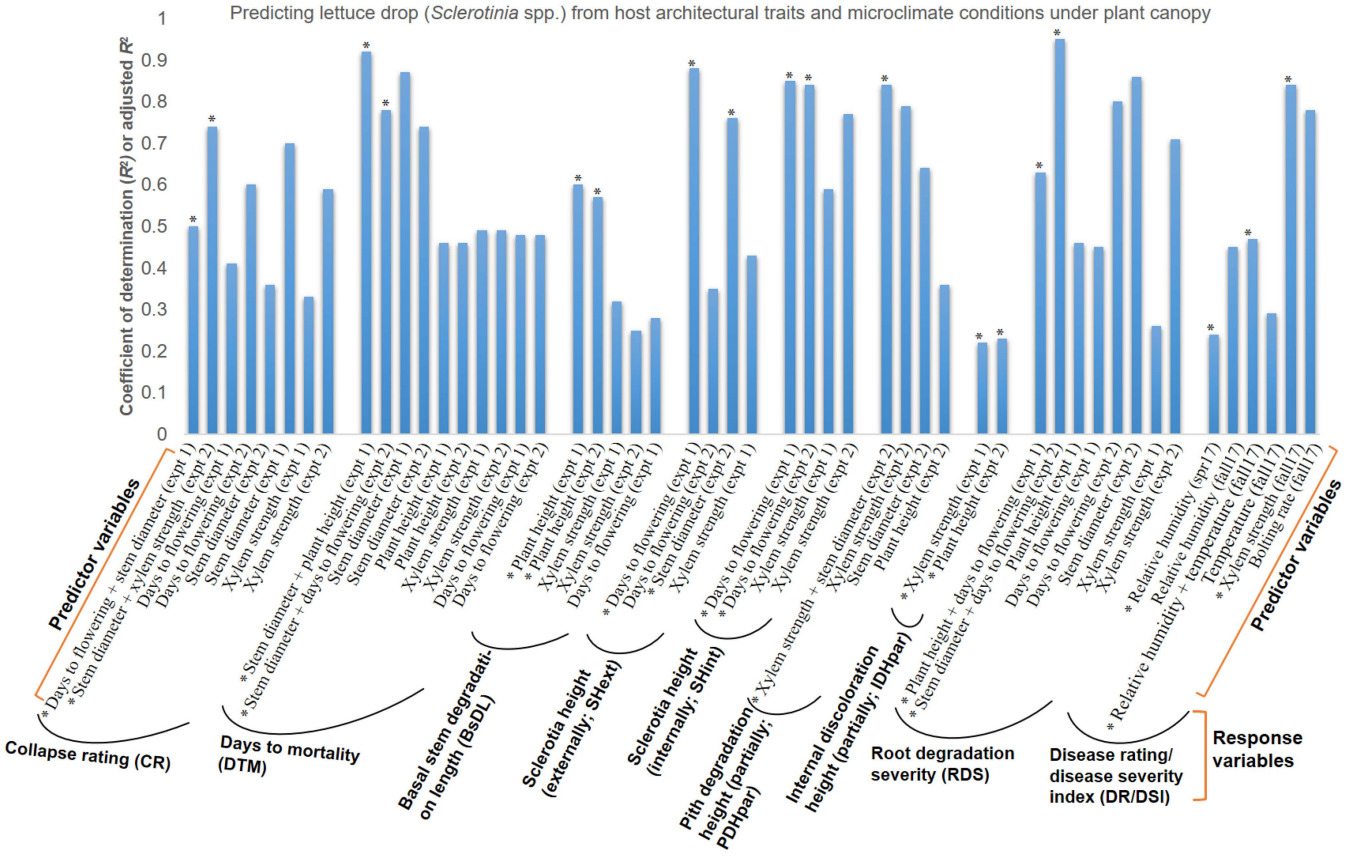

FIGURE 7
Prediction of lettuce drop (*Sclerotinia* spp.) from host plant architectural traits and microclimate conditions under plant canopy. *Y*-axis depicts the (adjusted) coefficient of determination (R^2) obtained from running (simple or multiple) linear regression procedures. Depicted on the *X*-axis are the predictor and response variables. Abbreviations: expt 1 and 2 refer to greenhouse experiments 1 and 2, respectively, and spr17 and fall17 refer to field experiments in spring and fall 2017, respectively. An asterisk (*) denotes the best predictors of lettuce drop measurements in univariate or multivariate models.

symptomatology and the possible role of the PAMR in defense reaction to the pathogen in 11-G99 (Supplementary Text S3).

The reduction in *A* rate was more rapid in the susceptible than in the tolerant genotype, confirming the differential response to infection. In Salinas plants, *A* was significantly decreased within 24 hpi with *S. minor* but remained intact until approximately 5 to 6 dpi in 11-G99. In the advanced stages of infection in 11-G99, *A* in the upper leaves was positively correlated with plant height, as observed under other conditions (Bishop 1991), and it was lower in lower leaves. In addition to the effect of leaf age (Field and Mooney 1983), this suggests postinfection feedback inhibition of photosynthesis, perhaps due to loss of sink capacity of their stems or rapid infection-related damage to the PSII enzyme at sites closer to primary infection (basal stem) (Bu et al. 2009; Cheng et al. 2016; Sharpe et al. 2009; Yang et al. 2014). In our study, *qP* or chlorophyll concentration was positively correlated with several disease-related variables, suggesting that both *qP* and chlorophyll concentration are strongly affected by the pathogen. In principle, lower leaf discoloration, as the first leaf-level symptom of infection, is caused by declining chlorophyll concentrations.

Microclimate conditions, primarily soil moisture and temperature, and morphological traits dictate lettuce drop. Although the severity of lettuce drop depends on the inherent characteristics of the host, the magnitude of the disease incidence is dictated by the environment. Lettuce genotypes with a prostrate growth habit, slow bolting, and large leaf area generally exhibit higher lettuce drop incidence owing to the possible modulations of the microclimate triggered by leaf canopies. According to Leach and Gilbert (1926), lettuce drop occurs only under very moist conditions created by rapidly spreading leaves of slow-bolting types. The authors concluded that the romaine type is less susceptible to lettuce drop because of its upright growth habit because it allows the soil around the base of the plant to remain dry. However, our data suggested that bolting may be required but not sufficient to impart lettuce drop resistance (Supplementary Text S4).

Host plant resistance to Sclerotinia diseases has been associated with plant architecture, including plant canopy, height, basal stem diameter, flowering time, maturity, lodging, and other developmental traits. Our work is the first to predict the genetic risk of lettuce basal stem to infection and degradation by *S. minor* and determine that basal stem strength is a key determinant of susceptibility or resistance and mortality in *Lactuca* spp. against *Sclerotinia* spp. Among the disease risk factors analyzed, xylem mechanical strength was the strongest predictor of lettuce drop severity (basal stem degradation), followed by the bolting rate. In contrast, RH or temperature did not predict DSI. Xylem mechanical strength as a risk factor explained most of the variations in basal stem degradation severity (84%), demonstrating that genetic factors can strongly determine the outcome of *Sclerotinia* infections. The potential role of stem strength in resistance breeding to *Sclerotinia* spp. is further strengthened because stem traits, including strength (Wang et al. 2018; Xiang et al. 2019), are strongly correlated with resistance to lodging. Lodging of infected plants is the usual outcome of Sclerotinia diseases (McCaghey et al. 2017). Besides, given the significantly softer stem tissues in the susceptible genotypes and the biological significance of mechanical barriers in host defense responses, we believe that stem strength is an important factor in the interaction of lettuce with *Sclerotinia* spp.

The possible contribution of stem "woodiness" in resistance to white mold caused by *S. sclerotiorum* has been recognized in pea (*Pisum sativum*) (Porter et al. 2009), where woodier stem pea lines were inclined to have shorter lesion lengths compared with other pea accessions from the *Pisum* core collection. In the study, pea stem diameter was determined as the best predictor of partial resistance based on lesion length to the pathogen. A correlation between stem diameter and stem lesion length in response to *S. sclerotiorum* infection also was detected in *Brassica* spp. (Li et al. 2006); however, Li et al. (2007) did not find a correlation between the two variables, indicating that the association varies based on experimental materials or test environments. Our results show that stem mechanical strength is stable across seasons and field and greenhouse environments; thus, it should be a more reliable trait to target in resistance breeding.

In summary, this study identified the production of *S. minor* sclerotium in or on uncollapsed and intact stems and peduncles of *Lactuca* plants, analogous to the overwintering mechanism of *Sclerotinia* pathogens in other host species. Analyses of the nature and extent of lettuce drop signs and symptoms integrating multiple approaches implicated a soft basal stem as a host susceptibility factor to lettuce drop. The symptomatology and pathophysiology experiments revealed discrete patterns of infection responses between modern cultivars and their landrace or wild relatives, yielding practical insights and enhancing our understanding of disease processes in the genus *Lactuca*. Regression analyses determined that developmental or basal stem biophysical features predict a relatively large amount of the variance in the resilience of host plants to basal stem and root degradations by *S. minor*, suggesting that genetics has a much larger influence on the outcome of lettuce–*Sclerotinia* spp. interaction. These findings implicate stem and crown mechanical strength as a possible resistance breeding target in lettuce, especially in crops intended for seed production, and in stem lettuce. The results also provide the prelude for the analysis of the biological basis of PAMR to *Sclerotinia* spp. in lettuce and other hosts.

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