Stemphylium Leaf Blight: A Re-Emerging Threat to Onion Production in Eastern North America

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Abstract

Stemphylium leaf blight (SLB), caused by *Stemphylium vesicarium*, is a foliar disease of onion worldwide, and has recently become an important disease in the northeastern United States and Ontario, Canada. The symptoms begin as small, tan to brown lesions on the leaves that can progress to defoliate plants. Crop loss occurs through reduced photosynthetic area, resulting in smaller, lower-quality bulbs. Leaf necrosis caused by SLB also can compromise bulb storage, as green leaves are required for the uptake of sprout inhibitors applied prior to harvest. The pathogen can overwinter on infested onion residue and infected volunteer plants. Asymptomatic weedy hosts near onion fields may also be a source of inoculum. Production of ascospores of the teleomorph (*Pleospora allii*) peaks in early spring in northeastern North America, often before the crop is planted, and declines rapidly as daily mean air temperatures rise. Conidia are usually present throughout the growing season. Application of fungicides is a standard practice for management of the complex of

fungi that can cause foliar diseases of onion in this region. Recent assessments have shown that populations of *S. vesicarium* in New York and Ontario are resistant to at least three single-site mode-of-action fungicides. Three disease prediction systems have been developed and evaluated that may enable growers to reduce the frequency and/or number of fungicide applications, but the loss of efficacious fungicides due to resistance development within *S. vesicarium* populations threatens sustainability. The lack of commercially acceptable onion cultivars with sufficient resistance to reduce the number of fungicides for SLB also limits the ability to manage SLB effectively. Integrated disease management strategies for SLB are essential to maintain profitable, sustainable onion production across eastern North America.

Keywords: fungi, vegetables, yield loss and economic impacts, disease management, etiology

Onion Production in New York State, U.S.A., and Ontario, Canada

New York State (NY) is the fifth largest producer of onion in the U.S.A., producing approximately 142,000 t of predominantly

pungent dry bulb onions from 2,800 ha (USDA NASS 2017), with some of the main production areas in the Elba muck in Orleans and Genesee counties, and in Oswego, Wayne, and Orange counties (Figs. 1 and 2B). Planting dates for early season maturing transplants, main season maturing transplants, and direct-seeded crops are late March to mid-April, mid-April to early June, and mid-April to mid-May, respectively. Early maturing transplants are harvested in mid-July to late August, with direct seeded and main season transplant crops harvested late August to late October. Approximately 25% of production in NY is from transplants and 75% is direct-seeded (C. A. Hoepting, *personal communication*). Bareroot transplants are sourced primarily from the southwestern United States (Leach et al. 2018). Aside from the 10% of the crop that is harvested early and sold immediately after harvest, the majority of the crop is stored and sold out of storage. Onions are typically machine-harvested within 5 to 14 days of undercutting, cured outdoors in stacks of 454-kg wooden pallet boxes, and then brought into cold storage between late September and early November. The bulbs are then stored in stacked boxes for 2 to 8 months (i.e., January to June).

In Canada, approximately 250,000 t of onions are produced from 5,700 ha, mostly in Ontario and Quebec (Statistics Canada 2020; Figs. 1B and 2A). In Ontario, onion is direct-seeded from mid-April to early May, and harvested from early August to late September. Approximately 10% of production is from plug transplants, which command a premium in the early market. Transplants are grown in

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Ontario greenhouses and are planted in late April to mid-May. Ontario onions are undercut and field cured for 2 to 21 days, then harvested into wood pallet boxes or crates and usually cured at 27 to 32°C for 1 to 3 days, followed by gradual cooling to 0°C and storage at 65% relative humidity (RH). Some of the crop is stored (~70%) and sold within 8 months of harvest (T. Blauel, *personal communication*).

Large-scale onion production in NY and Ontario has many similarities. The majority of production in both regions is on muck soil, a type of histosol that is high in decomposed organic matter, concentrated in relatively small regions where onion is a major crop. In the Holland Marsh region of Ontario, onion crops are often rotated with carrots (*Daucus carota* subsp. *sativus*) and other vegetables (Figs. 1 and 2B). In the muck soil regions in NY, continuous production of onion is common, although for farms that do practice crop rotation, onions are rotated most commonly with potato (*Solanum tuberosum*) and other field and vegetable crops (C. A. Hoepting, *personal communication*).

History and Importance

Origin and distribution of *Stemphylium* leaf blight. *Stemphylium* leaf blight (SLB) of onion is caused by the hemibiotrophic fungal pathogen *Stemphylium vesicarium* (Wallr.) E.G. Simmons (Sharma and Sharma 1999). The pathogen also causes important foliar diseases of other cultivated *Allium* spp., as well as a broad range of vegetable, field, ornamental, and tree fruit crops. In onion, the disease has been reported in Australia (Suheri and Price 2000b), Brazil (Mendes et al. 1998), Canada (Paibomesai et al. 2012), Cuba (Urtiaga 1986), Egypt (Hassan et al. 2007), Ethiopia (Gedefaw et al. 2019), India (Bhat et al. 2008; Gupta et al. 1994; Raghavendra Rao and Pavgi 1975), Japan (Misawa and Yasuoka 2012), Korea (Hye Sun and Seung Hun 2001), Mexico (Zapata-Sarmiento et al. 2020), the Netherlands (Köhl et al. 2009; Woudenberg et al. 2017), New Zealand (Singh 1977; Wright et al. 2019), South Africa (Aveling and Snyman 1993; Aveling et al. 1993), Spain (Basallote-Ureba et al. 1999), Taiwan (Pathak et al. 2001), Tonga (Dingley et al. 1981), Portugal (Tomaz and Lima 1988), the United States (Miller et al. 1978), and Venezuela (Cedeno et al. 2003; Urtiaga 1986) (Fig. 1A). In Welsh onion (*A. fistulosum*), SLB was reported in China (Tianyu 2009),

Japan (Shibata et al. 2000), Korea (Cho and Shin 2004; Yu 2001) and Taiwan (Pathak et al. 2001; Wang et al. 2021). In garlic (*A. sativum*), SLB has been reported in Australia (Suheri and Price 2000b), Brazil (Boiteux et al. 1994), Canada (M. R. McDonald, *unpublished data*), China (Woudenberg et al. 2017), Ethiopia (Gedefaw et al. 2019), Germany (Vaghefi et al. 2020), Korea (Hye Sun and Seung Hun 2001), Myanmar (Thaung 2008), South Africa (Aveling and Naude 1992), Spain (Basallote et al. 1993; Basallote-Ureba et al. 1999), and Turkey (Polat et al. 2012). Garlic leaf blight, caused by the closely related species, *S. solani*, has been reported in China (Zheng et al. 2008, 2010). Purple leaf blotch, also caused by *S. vesicarium*, has also been reported affecting leek (*A. ampeloprasum*) (Suheri and Price 2001).

The first report of SLB on onion in the United States was from Texas in 1976 (Miller et al. 1978) and the disease was subsequently reported in NY in 1985 (Shishkoff and Lorbeer 1987, 1989). A major epidemic of SLB occurred in NY in 1990, with SLB present in almost all fields surveyed across NY and causing severe foliar dieback in some fields (Lorbeer 1993). However, SLB occurred only sporadically in onion crops in NY in 1991 and 1992 and was rare in 1993 (Lorbeer 1993). Subsequently, SLB was considered of minor importance in the complex of foliar diseases affecting onion in NY until re-emergence of SLB around 2010 as the dominant foliar disease affecting large-scale onion production (Hay et al. 2019). Within the four major muck onion production regions in NY (Fig. 1B), SLB has become most severe in Elba. Neighboring regions of onion

Fig. 2. Large-scale onion production field on muck soil in **A**, Holland Marsh, ON, Canada (photo by M. R. McDonald), and **B**, Elba, NY, U.S.A. (photo by C. A. Hoepting).

Fig. 1. **A**, World map (light gray) and countries where *Stemphylium* leaf blight (*Stemphylium vesicarium*) has been reported on onion (*Allium cepa*) (dark gray); and **B**, geographical locations of major onion production regions in Ontario, Canada, and New York, U.S.A. Prepared by D. W. Heck.

production, including Michigan and Wisconsin in the U.S.A. (M. Hausbeck, *personal communication*), and Quebec in Canada (O. Carisse, *personal communication*), and other key onion production areas, e.g., Georgia (B. Dutta, *personal communication*), Idaho, and eastern Oregon (J. Woodhall, *personal communication*), have also reported increased incidence and severity of SLB in recent years.

In Canada, SLB was first identified in onion fields in the Holland Marsh, Ontario in 2008, and has since spread throughout the onion production regions of the province (Paibomesai et al. 2012; Stricker et al. 2021b). SLB is now the most damaging foliar disease in Ontario and Quebec. Historically, *Botrytis* leaf blight caused by *Botrytis squamosa* was the most destructive foliar fungal disease of onion in the region, but it is now rare to see symptoms of this disease, even when SLB incidence and severity are low. Therefore, SLB has recently become an important foliar disease of onion across eastern North America and in other major onion production areas. There has also been a recent outbreak of SLB in onion production in New Zealand (Wright et al. 2019).

Symptoms. SLB symptoms on *Allium* spp. typically become visible 7 to 14 days after inoculation (Basallote-Ureba et al. 1999; Misawa and Yasuoka 2012; Shishkoff and Lorbeer 1989). Early symptoms of SLB are pale brown to tan lesions that may initially appear water-soaked, are typically up to 2 to 3 cm in diameter, and usually develop first on the outer leaves (Ideta 1911; Miller and Schwartz 2008); or tan, mottled lesions, 0.5 to 4 cm diameter that first develop on inner (younger) leaves (Misawa 2008). Lesions are initially oval-shaped but can become spindle-shaped to ovate-elongate or even diffuse. The centers of the SLB lesions turn gray or dark olive-brown as profuse production of conidia occurs (Miller and Schwartz 2008; Misawa and Yasuoka 2012). In later stages of development of SLB, small yellow flecks or streaks may develop in the middle of the leaf (Saraswathi et al. 2017) that can progress acropetally to the leaf tips. The pathogen produces host-specific phytotoxins (Singh et al. 2000; Wolpert et al. 2002) that move in the leaf and likely are the cause of the chlorosis and necrosis that leads to leaf dieback and premature senescence (Basallote-Ureba et al. 1999; Raghavendra Rao and Pavgi 1975). Some SLB lesions may also have a pinkish margin surrounding the lesion (Hay et al. 2019; Raghavendra Rao and Pavgi 1975).

In NY, colonization and sporulation by *S. vesicarium* of necrotic tips and other tissues affected by dieback is common and is referred to as “dirty tips” (Fig. 3A). In leaves collected from three onion fields in NY in early July 2018 (6 to 7 true-leaf stage), between 66 and 92% of sporulation by *S. vesicarium* occurred on the top 20% of the leaves (F. S. Hay, *unpublished data*). Later in the season, leaves often exhibited dieback patterns, including necrosis developing from the leaf tip downward and progressing asymmetrically down the leaf. The individual spindle-shaped lesions that were observed at the base or middle of the leaf may have developed from splash-dispersed conidia or conidia washed from higher up the leaf (Figs. 3B to 3E). Typical progression of SLB in crops in NY has been categorized into eight stages (Table 1; Fig. 3).

Symptoms of SLB described in onion crops in Ontario, Canada, are similar to the descriptions by Ideta (1911) and Miller and Schwartz (2008), which differ slightly from those described in onion crops in NY (Table 1). Initial symptoms are water-soaked, chlorotic lesions that usually occur on the outer leaves. Chlorotic leaf tips are often present, but they are associated with normal leaf aging (Fig. 4A). The chlorosis spreads upward from the lesion to the leaf tip, resulting in leaf dieback. Sporulation normally occurs on the lesions on the lower portions of leaves and can develop on the leaf tips late in the season or when disease has become severe (Fig. 4B). Severe leaf dieback can develop when conditions are favorable for SLB development, but it is rare for plants to die prior to lodging of the tops.

For both regions, initial lesions normally develop on older leaves rather than young leaves. Older leaves are more susceptible than young leaves under controlled conditions, likely because older leaves have more leaf tip necrosis, which facilitates necrotrophic

colonization by the pathogen (Shishkoff and Lorbeer 1989; Tayviah 2017). However, other factors may also contribute to differences in the fields between infection of older versus younger leaves. For example, old leaves have been exposed to inoculum for longer than young leaves, and the protective cuticular wax on old leaves is more eroded over time as a result of abrasion by wind-blown soil particles or contact with other leaves. Also, older leaves are rarely upright in orientation, and are often parallel to the soil or partially bent. This orientation may result in more conidia intercepted by the leaves.

In direct-seeded onion crops in NY and Ontario, disease progress follows a general pattern of low incidence during May/June (<10%), followed by a rapid increase during July. Incidence in NY can be >80% by early August. In NY, severe SLB occurs when onion bulbs reach 4 to 5 cm diameter, at which time dense canopies have developed that reduce air movement and favor further development of SLB. This is generally accompanied by tip necrosis of at least 5 cm and dieback of the outer leaves.

SLB in NY onion fields appears to initiate at random, with no clear edge effect or disease foci (F. S. Hay, *unpublished data*). However, the disease becomes severe in patterns associated with differences in soil conditions, such as compaction around sprayer rows, low spots prone to flooding, or old creek beds that have different soil types than the surrounding field, indicating that abiotic stress favors SLB. In a controlled environment study in Ontario, drought stress did not increase the susceptibility of onion to SLB (Stricker 2021).

In NY, sporulation of *S. vesicarium* is commonly observed on necrotic tissue caused by contact herbicide injury, hail injury, or other foliar pathogens, but this occurs only occasionally in Ontario. SLB colonization of injured tissue tends to progress slowly prior to bulbing, and injured leaves often slough off the plant under dry conditions. After bulbing, SLB more commonly progresses from injured to healthy tissue, and young leaves often escape infection (F. S. Hay, *unpublished data*).

SLB symptoms may be confused with those caused by other foliar diseases affecting onion. The initial symptoms of purple blotch caused by *Alternaria porri* (Ellis) Cif. are also small spots that turn brown and are usually elliptical in shape (Suheri and Price 2000a).

Fig. 3. Stemphylium leaf blight symptoms on onion in Elba, NY. **A**, Necrosis at the leaf tips (“dirty tips”; stage 2 in Table 1); **B**, tan, oval lesions (stage 3 in Table 1); **C**, black and purple target spot lesions accompanied by generalized leaf dieback (stage 5 in Table 1); **D** and **E**, leaf dieback (photos by C. A. Hoepting).

Older purple blotch lesions usually develop a target spot appearance and are magenta to pink-purple. The lesion is usually surrounded by a chlorotic halo and the margin is often a deeper purple than typically observed with SLB. The presence of the distinctive conidia of *A. porri* in lesions is an important characteristic used to differentiate SLB from purple blotch. Purple blotch lesions form more readily on green leaf tissue than SLB. Often, SLB and purple blotch lesions coalesce, or one pathogen develops in the lesions caused by the other, and conidia of multiple foliar pathogens as well as secondary colonizers can develop in the same lesion.

Other foliar diseases that commonly affect onion in eastern North America include downy mildew caused by *Peronospora destructor* (Palti 1989), Botrytis leaf blight (Carisse et al. 2011), and *Iris yellow spot virus* (IYSV) (Bag et al. 2015). Diagnosis can be confusing because *S. vesicarium* can invade and produce profuse sporulation in lesions produced by these other foliar pathogens, especially those caused by downy mildew.

Crop loss. SLB can result in yield and quality loss of up to 90% in onion crops (FAO/IPGRI 1997; Lorbeer 1993; Miller et al. 1978; Raghavendra Rao and Pavgi 1975; Tomaz and Lima 1988). Defoliation from SLB reduces the photosynthetic area, resulting in smaller bulbs, and the tops may not lodge when the bulbs are mature (Fig. 5A; Brewster 2008). In field trials in NY, reduction of SLB through applications of selected fungicides increased bulb weight by 33 to 40%, and the number of jumbo grade (>7.6 cm diameter) bulbs by 29% (Hoepting 2018a, b). SLB has also been associated with up to 74% premature plant mortality when disease was severe (Hoepting 2017a). In the state of Georgia, losses of 60% of the *Vidalia* onion crop (estimated \$50 million loss) were attributed to SLB and a subsequent epidemic of other foliar diseases (du Toit and Inglis 2002). In contrast, there was no measurable yield or quality loss in recent field trials in Canada, even in 2015 when there was 96% disease severity prior to harvest (Fig. 5B; Stricker et al. 2021b). The lack of impact of SLB on yield may reflect infection occurring later in the growing season or slower disease development.

SLB generally leads to premature leaf senescence, making the crop more susceptible to postharvest losses (Paibomesai et al. 2012). Maleic hydrazide is a sprout inhibitor that is applied routinely prior to lodging to inhibit sprouting in storage (Brewster 2008; Isenberg et al. 1974). This product must be applied when the plant still has five to eight green leaves to provide sufficient uptake of maleic hydrazide into the bulbs. If the sprout inhibitor is not applied, the crop must be sold soon after harvest, often at a time of lower prices, leading to lower returns. Additionally, when onion leaves die prematurely and do not lodge, plants are at greater risk of bacterial bulb rots, which further reduces the quality and value of the stored crop (C. A. Hoepting, unpublished data).

Pathogen Biology

Taxonomy and identification. *S. vesicarium* was first described in 1801 by Christiaan Hendrik Persoon in Europe as *Sphaeria herbarum*. The currently accepted name for the anamorph is *Stemphylium*

vesicarium (Wallr.) E.G. Simmons, and the teleomorph is *Pleospora allii* (Rabenh.) Ces. & De Not., in the phylum Ascomycota, class Dothideomycetes, order Pleosporales, family Pleosporaceae (Woudenberg et al. 2017). The teleomorph was first reported in Varanasi, India (Raghavendra Rao and Pavgi 1975). Use of the anamorph (*Stemphylium*) nomenclature over that of the teleomorph has been recommended by the International Committee on the Taxonomy of Fungi (Rossman et al. 2015).

Stemphylium spp. are distinguished from other Hyphomycetes by the formation of dematiaceous multicelled conidia with longitudinal and transverse septa (phaeodictyosporous) and the presence of apically swollen, percurrently proliferating conidiogenous cells (Woudenberg et al. 2017). Conidiophores are straight or occasionally branched, pale to midbrown in color, up to 70 µm in length, and have dark bands or swellings where they give rise to the conidia. Conidiophores giving rise to conidia typically appear on infected tissue within 5 to 8 days after infection. Conidia are oblong to broadly oval and sometimes inequilateral in shape, pale to midbrown in color, with 1 to 5 transverse septa and 1 to 2 longitudinal/oblique septa (Fig. 6A). Conidia are often constricted at the major transverse septa and a basal scar is usually prominent. The conidial wall

Fig. 4. Typical *Stemphylium* leaf blight symptoms in onion plants in the Holland Marsh, ON, Canada. **A**, Necrotic tips, and **B**, necrotic lesions progressing up the leaves (photos provided by S. Stricker).

Fig. 5. **A**, Early symptoms of *Stemphylium* leaf blight (SLB) in onion in the Holland Marsh, ON, Canada. Cultivar on the right is more susceptible (photo by M. R. McDonald). **B**, Focus of SLB in Elba, NY (photo by C. A. Hoepting).

Table 1. Eight stages of *Stemphylium* leaf blight progression observed in onion in New York State

Stage	Symptom description
1	Tan necrosis (not associated with a lesion) at leaf tip or on senescing outer leaf tissue
2	Necrosis as described in stage 1 with black-colored <i>Stemphylium vesicarium</i> sporulation
3	Small, tan to brown, oval lesions on necrotic leaf tips and outer leaves (up to 2.5 cm diam.); necrosis progresses asymmetrically down the leaf
4	Oval tan to brown target spot lesions begin to turn black from sporulation of <i>S. vesicarium</i>
5	Black and purple, target spot lesions develop on necrotic tissue
6	New target spot lesions of any color develop on green tissue
7	Severe (>30%) leaf dieback occurs
8	Plants die prematurely and do not lodge normally

is conspicuously and densely verrucose. Conidia range in size from 27 to 42 × 12 to 22 µm and do not form in chains. *Stemphylium* spp. typically require exposure to near-ultraviolet light (NUV, 200 to 400 nm) to sporulate (Leach 1967; Raghavendra Rao and Pavgi 1975). Colony morphology on agar media may be cottony or velvety, and range from white to light to dark gray, or light olive green (Hassan et al. 2020b). The colony margin is typically whitish and may be filiform or entire. When grown under NUV light and a 12-h day length, concentric rings of conidiophores bearing light brown to black conidia form on agar media (Hassan et al. 2020a).

Pseudothecia are produced in or near SLB lesions on onion leaves. Pseudothecia are relatively large (100 to 500 µm diameter), black, pinhead-like structures that typically form toward the end of the growing season on diseased or symptomless leaves and inflorescence scapes (Misawa and Yasuoka 2012; Raghavendra Rao and Pavgi 1975). Asci are bitunicate and cylindrical to clavate, ranging from 110 to 170 × 24 to 38 µm (Basallote-Ureba et al. 1999; Misawa and Yasuoka 2012; Raghavendra Rao and Pavgi 1975). Ascospores are uniseriate, typically ellipsoidal and tapered to a point, pale yellow to brown, and range from 34 to 44 × 15 to 20 µm, with 3 to 7 transverse septa and 6 to 14 longitudinal septa, and a dark basal scar (Fig. 6B; Raghavendra Rao and Pavgi 1975; Simmons 1969). Exposure to cold temperatures for 3 to 6 months is often required for pseudothecia to mature and produce ascospores within asci (Miller and Schwartz 2008).

Both conidia and ascospores germinate to produce single or multiple germ tubes that terminate in bulbous terminal or intercalary appressoria on stomata or epidermal cells. Appressoria are most commonly single but may be double and, less commonly,

compound (Aveling and Snyman 1993; Falloon et al. 1987; Prados-Ligero et al. 2003).

The teleomorph, *Pleospora*, is polyphyletic, so identification to species requires a combination of morphology and gene sequence data (Woudenberg et al. 2017). The genomes of *S. vesicarium* isolates from pear (Gazzetti et al. 2019) and onion (Sharma et al. 2020) have been sequenced and assembled. Phylogenetically informative regions of the genome and genes for *Stemphylium* species identification are the internal transcribed spacers and 5.8S region of the nuclear ribosomal DNA (ITS), the intergenic spacer region between *vmaA* and *vpsA*, and the glyceraldehyde-3-phosphate (*gapdh*), translation elongation factor-1- α (*tef1*), and calmodulin (*cmdA*) genes (Inderbitzin et al. 2009; Vaghefi et al. 2020; Woudenberg et al. 2017). The ITS rDNA, *gapdh*, and *tef1* sequences have been used to separate *S. vesicarium* into a clade apart from other closely related *Stemphylium* spp., but were unable to differentiate *P. alfalfae*, *P. sedicola*, and *P. tomatonis* from *S. vesicarium* (Inderbitzin et al. 2009). A recent study has suggested these species be synonymized (Woudenberg et al. 2017). The cytochrome b (*cytB*) gene sequence can also be used to differentiate *S. vesicarium* from *S. botryosum* (Graf et al. 2016).

A monosporic isolate of *S. vesicarium* from onion in NY produced pseudothecia and ascospores in vitro (Shishkoff and Lorbeer 1989), which suggested that the species is homothallic (Inderbitzin et al. 2005). Subsequently, two isolates of *S. vesicarium* from NY were each shown to contain fused MAT1-1 and MAT1-2 genes in reverse orientation (Sharma et al. 2020), an arrangement also reported for some other *Stemphylium* species (Inderbitzin et al. 2005; Sharma et al. 2020).

The airborne spores of *Stemphylium* spp. can contribute to allergic reactions and hypersensitivity pneumonitis (Al-Doory and Ramsey 1987; Costa et al. 2006). *Stemphylium* spp. have also occasionally been associated with a fungal skin infection and have been isolated from abnormal toenails and a corneal ulcer in humans (Sutton et al. 1998). *S. vesicarium* was even identified as a contaminant in butter, but toxin production was not confirmed (Moubasher et al. 2018). However, a recent review concluded that *Stemphylium* spp. did not pose a risk to the health of humans or animals (Stricker et al. 2021a).

Host range. *S. vesicarium* can infect a broad range of plant species from several families, including many annual and perennial crop species (Farr and Rossman 2020). Non-*Allium* host crops include alfalfa (*Medicago sativa*; Lowe et al. 1987), parsley (*Petroselinum crispum*; Koike et al. 2013), radish (*Raphanus raphanistrum* subsp. *sativus*; Belisario et al. 2008), soybean (*Glycine max*; Darrag et al. 1982; Lamprecht et al. 1984), tomato (*Solanum lycopersicum*; Trinetta et al. 2013), and spinach (*Spinacia oleracea*; Liu et al. 2020). *S. vesicarium* also causes an economically important disease of asparagus (*Asparagus officinalis*; Bohlen-Janssen et al. 2018; Cunnington and Irvine 2005; Evans and Stephens 1984; Falloon et al. 1987; Foster et al. 2019; Menzies et al. 1991) and causes a postharvest fruit rot of mango (*Mangifera indica*; Ahmad et al. 2019). Additionally, *S. vesicarium* affects commercial production of chilli pepper (*Capsicum annuum*; Vitale et al. 2017) and sunflower (*Helianthus annuus*; Arzanlou et al. 2012). The fungus also causes brown spot of pear (*Pyrus communis*) in Europe (Köhl et al. 2009; Llorente and Montesinos 2006; Rossi et al. 2005a, b), which has not been identified in North America (Foster et al. 2019).

Variation among populations of *S. vesicarium* associated with differential pathogenicity and host specificity has been reported in many studies. For example, isolates from parsley were pathogenic to celery (*Apium graveolens*), carrot, and pear, but not leek, onion, spinach, or tomato (Koike et al. 2013). Similarly, isolates from asparagus were pathogenic on Japanese pear but not European pear (Singh et al. 1999). In pear orchards, some *S. vesicarium* isolates from fruit, leaves, or dead grass on the orchard floor were pathogenic and others, nonpathogenic to pear; whereas isolates from onion and asparagus were not pathogenic to pear, and formed separate clusters using multilocus sequencing and genetic diversity

Fig. 6. **A**, *Stemphylium vesicarium* sporulation (conidiophores) on diseased onion leaf tissue (inset conidia; scale bar = 10 µm); **B**, *Pleospora allii* pseudothecia in diseased onion leaf tissue. Inset shows ascospores in asci exuding from perithecia. Conidia marked with white arrows. Photos provided by S. Stricker and F. S. Hay.

analyses (Köhl et al. 2009). In contrast, *S. vesicarium* isolates from asparagus, onion, and garlic were pathogenic to all three crops (Basallote-Ureba et al. 1999); and isolates from Ontario onion and asparagus were pathogenic to asparagus crops and to wounded, but not unwounded, pear fruit (Foster et al. 2019). *S. vesicarium* isolated from lupin (*Lupinus angustifolius* L.) was pathogenic on lupin but not on faba bean, lentil, or alfalfa, whereas isolates collected from lentil only caused symptoms on lentil and not on faba bean, lupin, or alfalfa (Vaghefi et al. 2020). In addition, isolates collected from faba bean, chickpea, and alfalfa did not cause symptoms on any of the crops tested (Vaghefi et al. 2020). Of 44 *S. vesicarium* isolates collected as airborne spores in a pear orchard, only 5 (11%) were pathogenic on pear (Moragrega et al. 2018). These findings suggest substantial host range variation within and among *S. vesicarium* populations.

Life Cycle

Onion seed, transplants, and volunteer onions. Onion seed, transplants, and volunteer onion plants may act as sources of primary inoculum of *S. vesicarium* (Fig. 7). *S. vesicarium* can be carried on or in onion seed, and the pathogen is readily transmitted from infested seed to seedlings (Aveling et al. 1993; Stricker 2021). Infested seed was postulated as a factor in the SLB epidemic in NY in 1990 (Lorbeer 1993). However, most of the commercial onion seed used in North America and Europe is produced in arid environments where SLB is not a major pathogen but can be observed as a

secondary colonizer of lesions caused by other diseases (Gent et al. 2006). *S. vesicarium* was not detected in seed health assays of 17 commercial, nontreated onion seed lots (F. S. Hay, *unpublished data*). Also, most commercial onion seed for conventional production is treated with fungicides that reduce the risk of seed-to-seedling transmission. Therefore, infested seed is not currently considered a major source of primary inoculum in conventional onion production in the northeastern U.S.A. and Ontario, Canada.

Transplants have been identified as a significant source of IYSV and viruliferous thrips for direct-seeded crops in the Elba muck region of NY (Leach et al. 2018). Transplants may be a source of SLB, either by introducing infected transplants from the southwestern U.S.A. where transplants are produced and planted in NY, or by providing early planted crops in which SLB can establish, increase, and subsequently provide inoculum for nearby onion fields. In a transplant crop in Elba, NY, *S. vesicarium* was present on 90% of the leaves with senescent tips in late May, when direct-seeded crops were emerging (F. S. Hay, *unpublished data*). Onion transplants in Ontario are produced in local greenhouses and are relatively disease-free, so are not considered a potential source of inoculum for SLB. However, transplants may be planted before seeded onions emerge, so the pathogen could infect transplants before seeded onions emerge, extending the green bridge of host tissue for build-up of the pathogen population.

Volunteer onions within fields or in cull piles may also represent an important source of inoculum, especially in the absence of onion crop rotation. In two NY onion crops surveyed in late May 2020,

Fig. 7. Life cycle of *Stemphylium vesicarium* on onion (prepared by S. Stricker).

S. vesicarium was recovered from 80 to 88% of volunteer onion plants, even though the incidence in the surrounding crop was only 2 to 8% (F. S. Hay, *unpublished data*). This indicates that *S. vesicarium* had overwintered in the volunteers, or that the more rapidly developing volunteer plants acted as a green bridge for establishment of the pathogen in the crop.

Crop residue. The contribution of ascospores to primary inoculum on onion is poorly understood, but *S. vesicarium* overwinters as mycelia or pseudothecia on the leaf residue of several other crops (Basallote-Ureba et al. 1999; Katoch and Kumar 2017; Rossi and Pattori 2009; Simmons 1969). For example, in asparagus fields in California, pseudothecia on dried fern stalks from the previous season were a dominant source of inoculum for purple spot on spears in spring (Falloon et al. 1987). In pear orchards, pseudothecia overwintering on pear debris and dead leaves of grasses on the orchard floor released ascospores in spring that colonized debris and dried grasses, which in turn produced conidial inoculum for fruit infection (Llorente et al. 2011a; Rossi et al. 2005b, 2008).

The optimum temperature for the maturation of pseudothecia of *S. vesicarium* on garlic residue was between 5 and 10°C (Prados-Ligero et al. 1998). In the spring, ascospores that had developed over winter were dispersed from the pseudothecia when temperatures reached at least 14°C. Ascospore release on garlic coincided with frequent precipitation, temperatures between 10 and 21°C, and low vapor pressure deficit (Prados-Ligero et al. 1998, 2003). Similarly, pseudothecia on pear residue developed slowly, but only at high RH (>98%) with optimum temperature between 10 and 15°C (Llorente and Montesinos 2004).

The contribution of ascospores to primary inoculum on onion may differ between NY and Ontario. Pseudothecia typically form at the end of the growing season on leaves and stalks (Basallote-Ureba et al. 1999; Raghavendra Rao and Pavgi 1975). Immature pseudothecia are present in abundance on onion leaves late in the growing season in NY (Hay et al. 2019), and ascospores have been observed in pseudothecia on leaves kept in plastic bags in cool storage (5°C) for several weeks (F. S. Hay, *unpublished data*).

In Ontario, leaf residue rapidly broke down during winter, making pseudothecia difficult to detect. No pseudothecia were found in onion leaf residue in spring in one year (Gossen et al. 2021) but both pseudothecia and viable ascospores were present in residue on the soil surface in another year, and mycelia from buried samples produced viable conidia (Stricker 2021). In a study using spinach leaf residue, *S. vesicarium* pseudothecia formed only in those left on the soil surface and remaining intact after winter (du Toit and Derie 2003). The rapid breakdown of onion residue over winter may indicate that crop residue is not a dominant source of primary inoculum for SLB on onion in Ontario.

Spore trapping in Ontario demonstrated that ascospores were present at high numbers in onion fields early in April, but ascospore capture declined and was almost absent before the onion crops were seeded (Gossen et al. 2021). This indicated that *S. vesicarium* overwintered in the vicinity of onion fields, but conidia were likely the main source of inoculum driving SLB epidemics on onion in Ontario.

Alternative hosts. *S. vesicarium* may overwinter on weed residues (Raghavendra Rao and Pavgi 1975; Stricker 2021) and release ascospores in early spring. Recently, common weeds that occur adjacent to onion fields in Ontario (Stricker 2021) and NY (F. S. Hay, *unpublished data*) were identified as asymptomatic hosts of *S. vesicarium*, including common sow thistle (*Sonchus oleraceus*), yellow nutsedge (*Cyperus esculentus*), redroot pigweed (*Amaranthus retroflexus*), purslane (*Portulaca oleracea*), bull thistle (*Cirsium vulgare*), field horsetail (*Equisetum arvense*), field pennycress (*Thlapsi arvense*), and jimson weed (*Datura stramonium*) (Stricker 2021). It appears likely that some of the early-season inoculum in both regions is produced on overwintered residue of weeds infected the previous year. The relative importance of weeds as a source of inoculum is not known, and removal of such inoculum reservoirs may not be effective for controlling SLB in onion crops because airborne spores have the potential to travel great distances.

Secondary spread. High numbers of airborne conidia are found in onion crops during the growing season and increase as SLB incidence and severity increases (Gossen et al. 2021). This indicates a role of the airborne conidia in secondary spread of the disease. Splash dispersal from sporulating leaf tips appears to be important in NY. In Ontario, airborne dispersal may be more important, as sporulation on young (2 to 5 leaf) onion plants is not as common and sporulation is observed on older lesions before it is seen on necrotic leaf tips (Gossen et al. 2021). Onion thrips (*Thrips tabaci* Lindeman) have also been implicated as a vector of *S. vesicarium* conidia and feeding damage by thrips increased colonization of onion foliage by *S. vesicarium* (Leach et al. 2020). Both SLB and onion thrips can cause excessive leaf dieback when pressure is high.

Host-specific toxins. Host-specific toxins are compounds produced by plant pathogens that promote pathogen colonization and symptom development in susceptible host plant species by disrupting or killing host cells or tissues (Tsuge et al. 2013; Wolpert et al. 2002). Four secondary metabolites produced by *S. vesicarium* are host-specific toxins on at least some hosts: stemphylin, stemphyerylenol, stemphyloxin, and stemphol (Andersen et al. 1995). In pear, isolates of *S. vesicarium* produce one or more host-specific toxins immediately after conidial germination, which cause necrosis and death of plant cells (Singh et al. 1999, 2000; Wolpert et al. 2002).

Toxins are hypothesized to be involved in the pathogenesis of *S. vesicarium* to onion, but this has not been confirmed (Basallote-Ureba et al. 1999). The role of toxins produced by the pathogen in the development of SLB symptoms may explain observations connected with foliar lesions and leaf dieback. First, leaf necrosis associated with SLB is often preceded by development of distinct lesions. Also, inoculation of onion leaves with high concentrations of *S. vesicarium* conidia produces chlorosis and leaf blight rather than lesions (Lorbeer 1993). Studies in Ontario demonstrated small but reproducible differences in the susceptibility of onion cultivars to SLB (Foster et al. 2019). In some cases, there were differences among cultivars in the number of lesions that developed, which differed from the extent of leaf dieback observed within the same cultivars (Foster et al. 2019). Similarly, in NY fungicide trials, although most fungicide treatments resulted in similar results for both leaf dieback and SLB lesion counts (e.g., both measures of disease severity were high or low), some treatments resulted in severe leaf dieback but few SLB lesions, while other fungicide treatments resulted in limited leaf dieback and high numbers of SLB lesions (Hoepting et al. 2020a).

Factors Affecting SLB Epidemics

Temperature. The concentration of ascospores of *S. vesicarium* in air samples declined with increasing temperatures in spring in Ontario, but this association may result from ascospore depletion rather than the direct effect of temperature on ascospores (Gossen et al. 2021). Conidial release, however, was positively correlated with the number of days in the previous 10 days with temperatures of at least 15°C (Gossen et al. 2021). A similar relationship has been reported in garlic (Prados-Ligero et al. 2003; Suheri and Price 2001) and pear (Rossi et al. 2005a).

The optimal temperature for in vitro mycelial growth of four *S. vesicarium* isolates was 25°C (Bohlen-Janssen et al. 2018). The optimal temperature for germination and germ tube growth of ascospores was 31°C, and for conidia was 23 and 29°C, respectively (Bohlen-Janssen et al. 2018). On pear, infection was greatest at 23°C for fruit and 21°C on leaves (Montesinos et al. 1995). Infection by *S. vesicarium* on asparagus in New Zealand was greatest at 14°C (Menzies et al. 1991). The cardinal temperatures for infection of onion have not been quantified, but infection of onion leaves by *S. vesicarium* conidia can occur at temperatures between 10 and 26°C (Basallote-Ureba et al. 1999).

Moisture. On leek (Suheri and Price 2001), garlic (Prados-Ligero et al. 2003), and onion (Gossen et al. 2021), ascospore concentration increased 24 to 36 h after short periods of rainfall but declined with prolonged, heavy rainfall events. On onion in Ontario, the concentration of conidia increased substantially 2 to 72 h after rainfall, and the

amount of precipitation in the 10 days prior was positively associated with an increase in the daily number of conidia detected (Gossen et al. 2021). Increased release of conidia after rainfall has also been reported on garlic and other crops (Granke and Hausbeck 2012; Prados-Ligero et al. 2003; Suheri and Price 2001). Few to no *A. porri* conidia were captured during rain events (Meredith 1966), likely due to spores being washed out of the air and off lesions on plants. A recent study has the linked number of days with average vapor pressure deficit ≤ 0.5 kPa with increased airborne concentration of *S. vesicarium* spores (Stricker 2021).

At least 8 h of leaf wetness at 10°C was required for *S. vesicarium* infection of garlic leaves, and SLB severity increased with increasing air temperature (10 to 25°C) and leaf wetness duration (8 to 24 h) (Suheri and Price 2000b). In addition, infection of pear leaves by *S. vesicarium* can be halted irreversibly by a prolonged dry period (Llorente and Montesinos 2002).

Comparing SLB Epidemics in NY and Ontario

It is interesting to consider why SLB has become such an important disease of onion in the past 10 to 12 years in northeastern North America and why the disease develops differently in these two regions that are relatively close in proximity (160 km; Fig. 1B) and where onions are grown on the same soil type with many similarities in the production systems. Changes in the predominant onion cultivars grown in each region do not seem to be related to emergence of SLB as a predominant foliar disease in either region, as cultivars that have been planted for the last 20 or 30 years are no more resistant than cultivars grown more recently. For example, cvs. Stanley and Hamlet, which have been grown since prior to 2000, were assessed with other cultivars in 2015 and 2016 and were not less susceptible than other cultivars (Foster et al. 2019). The introduction of new contact herbicides for use by onion growers in Ontario, Canada, or the use of spray adjuvants with insecticides to control onion thrips has been considered as a contributing factor to the emergence of SLB in this region. However, field trials to determine if either of these factors contributed to more severe SLB found no significant relationships (M. R. McDonald, *unpublished data*). Another possible explanation for the overall increase in SLB in northeastern North America is warmer temperatures during the growing season as SLB is favored by warmer temperatures than Botrytis leaf blight (optimum temperatures for Botrytis leaf blight range from 18 to 22°C assuming the leaves are wet for 12 h; Alderman and Lacy 1983), but this hypothesis has not yet been tested.

The differences in SLB development observed between NY and Ontario are also interesting. The Elba area of NY is about 160 km to the south and slightly east of the Holland Marsh in Ontario, and on the south side of Lake Ontario (Fig. 1B). In NY, the onion growing season is slightly longer and the popular onion cultivars grown differ from those in Ontario, with a trend to later maturing cultivars in NY. The role of in-field inoculum must be considered, as onion monoculture is common in some of the NY production regions but uncommon in Ontario. However, the proximity of onion fields in the Holland Marsh means that inoculum from overwintering onion debris is always a potential source of inoculum for outbreaks of SLB in the next season. Onions in the Elba region of production in NY also tend to suffer from more damage from onion thrips and IYSV, possibly because this muck land is surrounded by many hay and wheat fields from which substantial numbers of onion thrips migrate into onion fields when these crops are harvested (C. A. Hoepting, *personal communication*). Elba also tends to be hotter and drier than muck lands in Wayne and Oswego counties, NY, that are closer to Lake Ontario. The combination of onion thrips, IYSV, and heat can put the onions in NY under greater stress than in Ontario. This may contribute to greater susceptibility of the more stressed onion crops to SLB. The significant proportion of onions grown in Elba from imported bare root transplants (~50%) may also contribute to the establishment of SLB in early spring in this region compared with in Ontario.

Disease Management

Cultural control. The use of certified seed and clean transplants is recommended for onion production in general, to avoid seedborne diseases and the insect pests and diseases that can be introduced on bare root transplants. Crop rotation with nonhost vegetables and cereals has been reported as an important cultural control method for SLB (Chand and Kumar 2016). Inoculum of *S. vesicarium* has been reduced in garlic and asparagus fields by removing or burying the plant debris at the end of the growing season (Johnson 1990; Katoch and Kumar 2017). In a NY study, onion grown with no onion leaf residue present from the previous fall, or where leaf residue was either buried or mechanically disrupted, exhibited delays in the initiation and progress of SLB relative to plots in which onion residue was applied to the soil surface the fall prior to planting (F. S. Hay, *unpublished data*). In pear orchards, the removal of plant residues from the orchard floor, especially when used in combination with other management tactics, reduced disease severity similar to that achieved with fungicides alone (Llorente et al. 2010a). Sanitation methods alone reduced disease incidence by 30 to 60%, while fungicides alone or in combination with sanitation achieved reduction of disease incidence in pear fruit of more than 60% (Moragrega et al. 2018).

The ability of *S. vesicarium* to colonize and sporulate on necrotic plant tissue of non-crop hosts represents yet another source of inoculum. For example, questions have been raised regarding the use of cereal companion crops for protecting against wind erosion in direct-seeded onion grown in muck soil. Barley or spring rye is either planted between the onion rows or broadcast as the onion crops are seeded. The rapid emergence of the cereal seedlings compared with onion seedlings allows the cereal plants to serve as a physical barrier that reduces damage caused by windblown soil. The companion crop is killed with herbicide before the plants get big enough to compete with the onion plants, i.e., usually the first true leaf stage, so a significant amount of dead leaf material is produced (Williams et al. 2015). Barley can be a host of *S. vesicarium* (Mehiar et al. 1976), but a survey in NY did not detect *S. vesicarium* in barley grown as a companion crop in onion fields (F. S. Hay, *unpublished data*). In Ontario, no symptoms developed after rye plants were inoculated with *S. vesicarium*, but the pathogen was recovered subsequently from senescent tissue (Foster et al. 2019).

Many of the common weed species found in and around onion fields can be asymptomatic hosts of *S. vesicarium* (Stricker 2021). Growers have many reasons for controlling weeds in and around fields, but the impact of weed management on outbreaks of SLB is not known. Also, moderate to severe infestations of weeds reduce air movement in the crop canopy, increasing relative humidity and leaf wetness duration, which increases the favorability of conditions for infection by foliar fungal pathogens like *S. vesicarium*.

Optimizing thrips management to reduce *S. vesicarium* secondary spread is also an important management recommendation in NY. Reducing thrips feeding on onion plants with insecticide applications decreased *S. vesicarium* colonization by 2.3 to 2.9 times, and SLB severity by 40 to 50%. Similarly, insecticide applications reduced SLB severity by 27% (Leach et al. 2020). In Ontario, the interaction of thrips and SLB is not as clear as a distinct contribution of thrips feeding damage in onion crops to severe SLB has not been observed (M. R. McDonald, *unpublished data*). Growers apply insecticides to manage thrips based on an integrated pest management program, independent of concerns about SLB.

Cultivars. There was some variation in SLB development among onion cultivars evaluated in field trials in the Holland Marsh, but most yellow onion cultivars were highly susceptible (Foster et al. 2019) and red onion cultivars were even more susceptible than yellow cultivars (M. R. McDonald, *unpublished data*). An onion cultivar developed in India called RO-1 had moderate resistance to SLB (Sharma and Sain 2003), and another study in India reported three cultivars with moderate resistance to SLB (Behera et al. 2013). Additionally, the bunching onion cultivar Pusa Soumya and the red onion cultivar Red Creole 2 exhibited moderate resistance to *S. vesicarium* in field trials conducted in India (Dangi et al. 2019). Resistance to

lesion development appears to be independent of susceptibility to development of leaf dieback symptoms (Foster et al. 2019).

There was no association between cultivar maturity, as indicated by published “days to harvest,” and susceptibility to SLB in field trials in Ontario (Tayviah 2017). Earlier maturing cultivars may occasionally have less incidence of SLB because early harvest results in some disease avoidance, but conversely, early maturing cultivars may be more susceptible because of rapid natural leaf senescence. Avoiding the confounding factors associated with differences in maturity when evaluating onion cultivars for SLB susceptibility is critical to identify true genetic resistance to SLB.

Some bunching green onion (*A. fistulosum*) cultivars are strongly to moderately resistant to *S. vesicarium* (Pathak et al. 2001). A breeding program crossed *A. fistulosum* and *A. cepa* to develop onion lines resistant to SLB (Pathak et al. 2001), but no resistant cultivars have yet been released. The progeny of a more recent cross of *A. fistulosum* and *A. cepa* also exhibited SLB resistance in a field trial (Kudryavtseva et al. 2019).

Fungicides. Effective management of SLB in onion crops in NY and in Ontario, Canada, has been based on multiple applications of mixtures of single-site mode-of-action fungicides that have moderate to high risk of resistance developing in populations of pathogens exposed to these fungicides (Hay et al. 2019; Pethybridge et al. 2016). Fungicides with multisite mode of action, such as chlorothalonil (Fungicide Resistance Action Committee [FRAC] group M5) or mancozeb (FRAC M3), have not been effective at reducing losses to SLB in onion crops in NY (Hoepting 2019; Hoepting et al. 2020b, c). In Ontario, chlorothalonil suppressed SLB in field trials conducted in 2011 and 2012 (Stricker et al. 2021b), but testing was discontinued when the number of applications permitted for this product in onion crops in Ontario was reduced by the Pesticide Management Regulatory Agency of Canada. Mancozeb has not been tested for the management of SLB in Ontario since 2013 (Stricker et al. 2021b).

Fungicide applications for management of SLB in onion in both NY and Ontario are often initiated by growers at the beginning of July and occur at 7- to 10-day intervals until the crop lodges, without regard to weather-based risk assessment (Pethybridge et al. 2016). This leads to 6 to 8 fungicide applications for SLB control each season. Growers in both regions have observed the lack of effective fungicides for SLB management (Hay et al. 2019; Hoepting and Pethybridge 2016; Pethybridge et al. 2016).

Best management practices for fungicides recommended in onion production include rotation of products from different FRAC groups, limiting the number of applications of particular FRAC groups within a season (to, ideally, no more than three applications per FRAC group), and using premixed fungicides (Hay et al. 2019). NY onion growers have diligently adopted these vigorous recommendations. In Ontario, Canada, the number of fungicides from different FRAC groups is quite limited. As a result, Ontario producers often apply only two fungicide products per season. However, repeated exposure of *S. vesicarium* to fungicides in specific FRAC groups within and between cropping seasons is inevitable in both production regions.

Fungicides containing iprodione (FRAC 2), azoxystrobin (FRAC 11), boscalid (FRAC 7), pyrimethanil (FRAC 9), and propiconazole (FRAC 3) have been registered in NY on onion for many years. Field trials in NY and Ontario have been conducted regularly to screen fungicides for efficacy against SLB. In NY, fungicides containing azoxystrobin or pyraclostrobin (FRAC 11) were ineffective (Hoepting 2016; Hoepting and Pethybridge 2016). Similarly, boscalid (FRAC 7) was highly effective in early trials but declined in efficacy by 2017 (Hoepting 2016, 2017b, 2019). Field trials conducted from 2017 to 2020 have identified reduced performance of iprodione (FRAC 2) and fluopyram + pyrimethanil (FRAC 7 + 9) compared with previous years (Hoepting 2018a, 2019; Hoepting et al. 2020a, b, 2021a, b). The efficacy of FRAC 7-based fungicides containing active ingredients such as fluxapyroxad has also declined rapidly (Hoepting 2017b, 2018a, 2019; Hoepting et al. 2020a, b, 2021a, b). In a 2020 field trial, plots receiving difenoconazole + cyprodinil (FRAC 3 + 9), difenoconazole + azoxystrobin

(FRAC 3 + 11), and propiconazole (FRAC 3) were not different than the nontreated control. The only treatments that were effective at controlling SLB were tebuconazole + phosphorous acid (FRAC 3 + P07), tank mixes of two FRAC 3 products and fluopyram + pyrimethanil + iprodione (Hoepting et al. 2021a, b).

Field trials in Ontario from 2013 to 2019 also demonstrated declining efficacy of fungicides against SLB. Azoxystrobin + difenoconazole (FRAC 11 + 3) and fluopyram + pyrimethanil (FRAC 7 + 9) were effective in trials from 2011 to 2013. However, from 2014 to 2019, these products did not reduce SLB severity compared with the nontreated control plots. It was also concerning that the fungicide containing cyprodinil + fludioxonil (FRAC 9 + 12), both of which are considered to have low to medium risk of developing fungicide resistance, reduced SLB severity in a trial in 2011, but not in field trials from 2012 to 2015. In recent trials, no fungicide provided effective suppression of SLB (Stricker et al. 2021b).

Fungicide resistance. *S. vesicarium* is at high risk for developing fungicide resistance because it has a short asexual reproductive cycle, multiple generations per cropping season, and the ability to produce many airborne spores through sexual and asexual reproduction each year (Gossen et al. 2021). Resistance to iprodione (FRAC 2) was demonstrated for brown spot of pear (Alberoni et al. 2005) and was associated with mutations in the histidine kinase gene (Alberoni et al. 2010). In NY onion fields, there was little evidence of resistance to iprodione based on in vitro testing (Hay et al. 2019). Field observations indicated moderate reductions in SLB caused by applications of iprodione until 2018 when field performance declined (Hoepting 2019). Similarly, there was little evidence of resistance to the demethylation inhibitor, difenoconazole (FRAC 3) in *S. vesicarium* isolates collected from onion fields in NY in 2016 and 2018 (Hay et al. 2019), and fungicides utilized in onion production with active ingredients in FRAC 3 (difenoconazole, propiconazole, and tebuconazole) provided effective SLB reduction in field trials conducted from 2018 and 2019. However, in a 2020 field trial in NY, fungicides containing difenoconazole and propiconazole had no greater efficacy against SLB than the nontreated control plots (Hoepting et al. 2021a, b), which suggests the pathogen population is developing resistance to FRAC 3 fungicides. In Ontario, >90% of isolates tested were sensitive to difenoconazole in a mycelial-growth assay (Stricker 2021). However, difenoconazole does not inhibit conidial germination, and fungicides containing difenoconazole have not provided SLB suppression in field trials in Ontario since 2013 (Stricker et al. 2021b).

Cyprodinil and pyrimethanil (FRAC 9) are commonly used in NY onion production (C. A. Hoepting, *unpublished data*). In vitro mycelial growth assays have provided evidence for insensitivity within *S. vesicarium* populations (Hay et al. 2019), which have been supported by reports of declining efficacy in the field (Hoepting 2018a, b, 2019; Hoepting et al. 2020b). Laboratory testing has also identified insensitivity to FRAC 9 fungicides in *S. vesicarium* from onion crops in Ontario (Stricker et al. 2021b).

Most of the *S. vesicarium* isolates collected from diseased onion leaves in NY in 2015 and 2016 were sensitive to the succinate dehydrogenase inhibitor (SDHI; FRAC 7) fungicides fluopyram and fluxapyroxad, but over half of the isolates were resistant to another SDHI fungicide, boscalid (Hay et al. 2019), for which declining efficacy had been noted in the field (Hoepting 2018a). Recent testing has also indicated a shift toward insensitivity to fluopyram in *S. vesicarium* isolates from Ontario (Stricker 2021), and insensitivity to fluopyram and fluxapyroxad among isolates in NY (F. S. Hay, *unpublished data*), which have also been associated with reduced efficacy against SLB in the field (Hoepting et al. 2020a, b, 2021a, b).

Resistance to FRAC 11 fungicides has been reported in *S. vesicarium* isolates from pear in Italy (Alberoni et al. 2010). In NY onion fields, azoxystrobin and pyraclostrobin (FRAC 11) have exhibited poor efficacy against SLB since 2015 (Hoepting 2016). Subsequently, resistance to azoxystrobin was identified in a high proportion (70%) of *S. vesicarium* isolates based on in vitro tests (Hay et al. 2019). This resistance was associated with the G143A mutation

within the *cytochrome b* gene (Hay et al. 2019). Cross-resistance between azoxystrobin and pyraclostrobin was also documented (Hay et al. 2019). Similarly, in the Holland Marsh area of Ontario, in vitro testing showed that 79% of 48 *S. vesicarium* isolates were resistant to azoxystrobin and 48% of 42 isolates were resistant to both azoxystrobin and pyrimethanil (Stricker et al. 2021b).

Resistance to FRAC 2, 7, 9, and 11 fungicides in the *S. vesicarium* populations in onion fields in NY and Ontario has led to increased use of fungicides primarily in FRAC 3 and increased selection pressure for resistance. Identification of efficacious fungicides in other FRAC groups would be beneficial for managing fungicide resistance. In Italian pear orchards, captan (FRAC M4), captan + tebuconazole (FRAC M4 + 3), boscalid (FRAC 7), fludioxonil (FRAC 12), and fluazinam (FRAC 29) have provided effective SLB reduction (Brunelli et al. 2014). In contrast, although mycelial growth of *S. vesicarium* was inhibited by fludioxonil in vitro, fungicides containing fludioxonil or fluazinam had poor efficacy against SLB in the field (Hoepting 2016; Hoepting et al. 2020a). None of these fungicides, except boscalid, is registered for foliar applications for onion crops in Ontario (Ontario Ministry of Agriculture, Food and Rural Affairs 2021).

Disease forecasting. Onion growers often make fungicide applications to manage SLB every 7 to 14 days (C. A. Hoepting, *personal communication*). Therefore, there is considerable scope to utilize disease forecasting models to reduce the number of sprays while providing the same or better disease suppression. Also, repeated fungicide applications increase the risk of fungicide resistance developing in the pathogen population. Therefore, reducing the number of applications should extend the useful life of a fungicide for control of SLB (Stricker et al. 2021b).

Until recently, growers in Ontario began fungicide applications when the disease was first reported in the local area, which typically coincides with the fourth true-leaf stage of growth (Tayviah 2017). More recently, applications have been initiated when the local pest management program indicates that weather conditions are conducive to disease development (T. Blauel, *personal communication*). In a recent study in Ontario, six forecasting models for SLB severity were assessed over four years (Stricker et al. 2021b). SLB severity in plots managed according to the models was either equal to or less than that observed in plots that received the weekly spray program, generally with fewer fungicide applications. In each of the four years, applications of fungicides according to the TOMcast model (Madden et al. 1978) reduced the number of applications by one or two compared with a weekly spray program. TOMcast is a model developed for tomato growers in Ontario to forecast diseases caused by *Septoria lycopersici* and *Colletotrichum coccodes* (Pitblado 1992). The TOMcast model is a modification of an earlier FAST (forecasting *Alternaria solani* on tomato) model developed by Madden et al. (1978). In both systems, disease severity values (DSVs) are calculated based on leaf wetness duration and the average temperature during the wet period, and fungicide sprays are recommended when cumulative DSVs meet or exceed a set threshold value (Madden et al. 1978). In field trials in Ontario, SLB severity in plots treated with fungicide applications according to TOMcast were not significantly different from those applied on a regular basis (Stricker et al. 2021b). Subsequent assessment showed that the *S. vesicarium* population at this site was largely resistant to most of the active ingredients applied, which explained the lack of reduction in SLB severity or differences in yield resulting from fungicide applications regardless of the forecasting system used (Stricker et al. 2021b). The only treatment that significantly reduced disease severity was a seed treatment containing the fungicide penflufen (FRAC 7) in combination with calendar-based foliar fungicide applications (Stricker et al. 2021b).

Forecasting models that have been developed for brown spot of pear may also have utility in onion. The brown spot of pear forecasting system (BSPcast) was developed for predicting infections of *S. vesicarium* on pear (Montesinos et al. 1995). It has been implemented as a warning system in Spain, Italy, Belgium, The Netherlands, and Portugal (Llorente et al. 2011b; Llorente and Montesinos

2006). When tested in onion field trials in Ontario, applications of fungicides based on BSPcast reduced applications by one or two sprays for SLB but BSPcast was no more effective than TOMcast (Stricker et al. 2021b).

The PAMcast (*Pleospora allii* maturation forecast) model was developed to relate environmental conditions in pear orchards to maturation of pseudothecia, which release initial inoculum in spring (Llorente and Montesinos 2004). This model has been evaluated in Spain and used to predict ascospore release to establish the date to begin evaluation using BSPcast for scheduling fungicides (Llorente and Montesinos 2004). However, release of ascospores of *P. allii* in Ontario was largely complete prior to the onion crops being planted, so timing of ascospore release is unlikely to be important in onion cropping systems.

The STREP forecasting system was also developed for brown spot of pear based on factors related to the host (cultivar susceptibility and phenological age), pathogen (level of inoculum), environmental conditions (wetness, temperature, and relative humidity), and the efficacy of specific fungicides for brown spot management (Llorente et al. 2000a). STREP reduced fungicide applications in pear orchards by 20 to 50% and achieved similar levels of control to a prophylactic spray program (Llorente et al. 2000b). Considerably more research is needed to determine if this forecasting system can be applied to effectively manage SLB in onion.

Biological control. Biofungicides represent a potential option to augment or replace synthetic fungicides for control of SLB in onion crops in the long term. Integrated management of *S. vesicarium* on pear in Europe includes removal of leaf litter before winter to reduce inoculum potential, and application of biopesticides containing *Trichoderma* spp. to the soil from February to May (Llorente et al. 2010b; Rossi and Patteri 2009). The *Trichoderma*-based products reduced conidial production on dead grass species in field plots by 50% (Rossi and Patteri 2009) and reduced subsequent infection of pear fruit (Ponti et al. 1993). Application of two bacterial species, *Pseudomonas fluorescens* and *Pantoea agglomerans*, also provided moderate reduction of brown spot of pear (Montesinos et al. 1996). However, some strains of *P. agglomerans* are highly pathogenic on onion (Schwartz and Mohan 2008).

In onion, application of *T. harzianum* reduced SLB severity by 26% in Egypt (Hussein et al. 2007) and reduced severity by 68% when applied prior to inoculation with *S. vesicarium* (Abo-Elyousr et al. 2017). Application of *T. atroviride* on onion in Ontario did not provide SLB suppression in each of two years compared with the non-treated control plots (Stricker et al. 2021b). Trials are continuing to evaluate *T. atroviride* applications alternated with conventional fungicides. In vitro studies have demonstrated reduced mycelial growth of *S. vesicarium* in dual culture with *T. asperellum* (Zapata-Sarmiento et al. 2020) or *Bacillus subtilis* (Al-Badri et al. 2020). Further, inoculation of onions with *T. asperellum* followed by *S. vesicarium* decreased disease severity by nearly 50% under controlled environmental conditions (Zapata-Sarmiento et al. 2020).

Biochemical-based products that reduce disease by stimulating the expression of defense mechanisms (Choudhary et al. 2007) have also been evaluated for SLB management. In one study, foliar application of salicylic acid reduced SLB severity in onion by up to 40% (Abo-Elyousr et al. 2009). A recent study has demonstrated that propolis extracts inhibited in vitro growth of *S. vesicarium* (Loebler et al. 2020). Synthetic antimicrobial peptides reduced brown spot of pear by 42 to 60% in pot studies, and 38% in field trials (Puig et al. 2015). Both of these types of products have yet to be tested in the field for SLB on onion. Various products listed for organic use by the Organic Materials Review Institute have been assessed in the field over two onion seasons in NY but had little or no efficacy against SLB on onion (F. S. Hay, *unpublished data*). Materials assessed include copper hydroxide, copper oxychloride, potassium silicate, neem oil, *Bacillus amyloliquefaciens*, *B. mycoides*, *B. subtilis*, and extract of giant knotweed (*Reynoutria sachaliensis*). Polyoxin-D zinc salt was associated with a slight reduction in SLB incidence but had no effect on SLB severity or onion yield (F. S. Hay, *unpublished data*). It is important to note that the formulation

technology for many biofungicides needs to be improved before the use of these products can become a practical option for field crops, like onion.

Moving Forward: Gaps and Challenges

This review has shown that SLB represents an important constraint to onion production in northeastern North America, and many challenges remain to predict and manage this disease effectively. The authors do not anticipate that highly effective resistance to SLB will be available in commercial cultivars for onion producers in the foreseeable future. Small differences in susceptibility among cultivars have been identified, but severe disease can still develop on the less susceptible cultivars (Foster et al. 2019; F. S. Hay, *unpublished data*).

Given the rapidly dwindling number of fungicides that provide effective SLB management, there is an urgent need to identify new and efficacious fungicides in different FRAC groups to replace those lost to fungicide resistance in *S. vesicarium* populations. In NY, the most effective fungicide groups for managing SLB is FRAC 3. The observation that a fungicide seed treatment reduced SLB severity suggested that protecting seedlings from early infection may reduce epidemic development (Stricker et al. 2021a). Understanding SLB dynamics early in the season, and whether epidemics can be reduced with early season applications of fungicides is warranted, especially in Elba, NY, where 50% of the onion production is from transplanted onions as they may serve as a green bridge for SLB between seasons. Spore trapping studies could show the temporal dynamics in ascospore and conidia release, and the potential overlap of these inoculum sources with early crop establishment. Since resistance to FRAC 7 fungicides is prevalent in *S. vesicarium* populations in NY, it is unlikely that penflufen seed treatment will be effective at reducing SLB outbreaks, but early season applications of effective fungicides should be investigated.

Developing new synthetic fungicides is a slow process, and it is even more difficult to discover new modes of action. However, it is critical that the genetic mutations associated with resistance of *S. vesicarium* populations pathogenic on onion to individual FRAC groups are characterized and cross-resistance documented to evaluate strategies for resistance management. Biofungicides and biochemical activators have either been ineffective or considerably less effective than conventional fungicides in onion field trials on SLB management to date. However, they may have a place in fungicide programs when SLB pressure is low early in the season or when a predictive model indicates low SLB pressure. They may also be effective at guarding against or delaying the onset of fungicide resistance when coapplied with conventional fungicides, especially those that have high risk for fungicide resistance.

As new disease management products are introduced for control of SLB in onion crops, extension and outreach to growers will continue to be important to emphasize management practices that will extend the life of these new products and prevent the development of resistance for as long as possible. The approach should include alternating fungicides with different modes of action, avoiding the use of fungicides with high levels of resistance present in the pathogen population, and reducing the number of sprays or switching to biofungicides, plant defense activators, or protectants (e.g., FRAC M1 or M5) in low-risk periods. Meeting this challenge should also involve development and validation of an SLB forecasting system for onion that recommends applications based on disease risk to reduce the number of applications of fungicides with single-site modes of action, which have moderate to high risk of resistance development where possible.

Identification of important sources of inoculum that initiate SLB outbreaks in onion crops in the spring is required for effective management of the disease. There could be many sources of initial inoculum of *S. vesicarium*, including overwintering volunteer onions, infected crop residue in the soil, dead or overwintering weed species, cover crops, and ornamental or wild host species in the surrounding area. As a polycyclic disease, SLB has the potential for rapid

increase of secondary inoculum. Overwintering inoculum is especially important in NY onion fields, where continuous cultivation of onion for many years in the same fields has exacerbated this polycyclic disease in the crop season and over multiple crop seasons. Even when crop rotation out of onion is the normal practice in large-scale Ontario onion production in muck soils, the onion fields are located side by side and inoculum can easily move between fields. Methods to reduce initial inoculum through improved weed and residue management, that delay initial establishment of infection, merit study. Onion production in both regions occurs mostly on localized pockets of muck soil, so the activities of one grower can affect adjacent growers because inoculum dispersal is regional.

The comparison of symptoms and development of SLB in NY and Ontario onion production has demonstrated there is still much to be discovered about SLB on onion. Even though the production systems are similar in soil type and agronomic methods, and are only located 160 km apart, symptoms that develop initially can be very different, as can be the symptoms associated with severe disease and the effects on bulb yield. The resurgence of SLB in NY over the past 5 to 10 years, and the emergence of SLB in Ontario, Canada, occurred about the same time, and problems with fungicide resistance are very similar in the two regions.

The authors note that both biotic and abiotic stresses may contribute to higher SLB in NY. Onions in the Elba muck regions of production in NY tend to experience more damage from onion thrips and IYSV, possibly because this muck land is surrounded by many hay and wheat fields from which substantial numbers of onion thrips migrate into onion fields when these crops are harvested. Elba also tends to be hotter and drier than muck lands in Wayne and Oswego counties, NY, which are closer to Lake Ontario. The combination of onion thrips, IYSV, and heat can put the onions in NY under greater stress than in Ontario. This may contribute to greater susceptibility to SLB. The significant proportion of onions grown in Elba from imported bare root transplants (~50%) may also contribute to SLB becoming established in onion crops in early spring in this region compared with in Ontario. Further comparisons of environmental conditions and production practices may yield valuable information on the biology, epidemiology, and management of this important disease.

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Frank Hay

Dr. Frank Hay is a senior extension associate in plant pathology at Cornell AgriTech, Cornell University, Geneva, NY. He completed his Bachelor of Horticultural Science degree with first class honors and Ph.D. in plant pathology at Lincoln University in Christchurch, New Zealand. He has held research positions at AgResearch, Palmerston North, New Zealand, and vegetable plant pathologist and group leader at the (previously) Tasmanian Institute of Agricultural Research, Australia. Dr. Hay has over 20 years' experience in fungal plant pathology and nematology across a broad range of crops including hops and pyrethrum. His program at Cornell University specializes in diseases affecting the profitability and sustainability of the New York onion and garlic industries.

Sara Stricker

Dr. Sara Stricker is a plant pathologist working as the communications coordinator at the Guelph Turfgrass Institute. She aims to make turfgrass research interesting and accessible to the industry and the public. Sara obtained her B.Sc., M.Sc., and Ph.D. degrees at the University of Guelph and completed a Bachelor of Education at Western University. She has conducted research on foliar diseases including tar spot of maple, Stemphylium leaf spot of onion, and Microdochium patch of creeping bentgrass.

Bruce D. Gossen

Dr. Bruce D. Gossen graduated with a Ph.D. in plant pathology from the University of Saskatchewan in 1985. Since then, he has been employed as a research scientist with Agriculture & Agri-Food Canada at Saskatoon, SK, specializing in management of diseases of field crops. Over the course of his career, he has worked on diseases of forages and turf, cereals, pulse crops, canola, and even vegetables. He has published more than 170 papers in refereed journals, plus hundreds of other articles and presentations. He has had a leadership role in many organizations, including a term as president of the Canadian Phytopathological Society, and has received numerous awards for his work, including two Golden Harvest Awards from AAFC and the Award for Outstanding Research from the Canadian Phytopathological Society. He currently leads studies on clubroot of canola and on root rot of field pea with colleagues across Canada and the U.S.A., and he continues to be active in supervision of graduate students and mentoring post-doctoral fellows.

Mary Ruth McDonald

Dr. McDonald is a professor in the Department of Plant Agriculture at the University of Guelph, Ontario, Canada. She has a Ph.D. (1994) from the University of Guelph specializing in plant pathology. Dr. McDonald started her career as the integrated pest management specialist for onions and carrots with the Ontario Ministry of Agriculture and Food, and she has continued to conduct research on many aspects of disease and insect pest biology and management with a focus on vegetable crops. Her research program provides integrated pest management scouting and information for growers of onions and other vegetables in the Holland Marsh and other parts of the province of Ontario. This has been operating since 2004 and allows for rapid identification of crop protection problems and rapid integration of research results into the IPM program. Prof. McDonald has been a member of the American Phytopathological Society for three decades and is a long time member and past president of the Canadian Phytopathological Society. She has received college, national, and international awards for excellence in research, extension, and integrated pest management, including the International IPM Award of Excellence (2015) and the Award for Outstanding Research from the Canadian Phytopathological Society (2021).

Daniel Heck

Daniel Winter Heck was born in Paraná State, Brazil. He received a B.Sc. in agronomy in 2013 from the Federal University of Technology - Paraná (UTFPR), an M.Sc. in crop protection in 2015 from the State University of São Paulo "Júlio de Mesquita Filho" (UNESP), and in 2019 received his D.Sc. in plant pathology from the Federal University of Viçosa (UFV), Brazil. His studies have been focused on quantitative epidemiology and the management of soilborne and foliar diseases on multiple crops. He conducted field surveys and experiments to fill knowledge gaps on the epidemiology of Fusarium wilt of bananas caused by race 1 (*Fusarium oxysporum* f. sp. *cubense*) and strategic management of Stemphylium leaf blight (*Stemphylium vesicarium*) on onions. He has experience in experimental design, molecular analysis, fungicide resistance, population genetics studies, and alternative, biological, and chemical management of plant diseases.

Christy Hoepting

Christy Hoepting is a vegetable specialist with the Cornell Vegetable Program of the Regional Cornell Cooperative Extension in western New York, a position she has held since 2001. She conducts on-farm applied research projects and demonstrations, and educational programming in onions, cabbage, broccoli, and garlic. Her areas of interest include all aspects of muck onion production with emphasis on weed management using herbicide programs, control of Stemphylium leaf blight featuring fungicide resistance management, control of onion bulb rot, onion variety evaluation, and nitrogen dynamics. She also focuses on weed management with herbicides in cabbage, management of swede midge in small-scale brassicas, Alternaria leaf spot/head rot in broccoli, and post-harvest practices in garlic. Her muck onion scouting program measures in real time the efficacy of growers' spray programs and is credited for unprecedented grower adoption of integrated pest management practices in New York's most intensively grown crop. She has a B.Sc. (1997) degree in environmental toxicology and an M.Sc. (2001) in plant pathology and applied entomology from the University of Guelph. In 2018, she was the recipient of the Cornell College of Agriculture and Life Sciences Award for Outstanding Accomplishments in Extension and Outreach.

Sandeep Sharma

Sandeep Sharma completed his Ph.D. in cell and molecular biology (plant pathology) from the University of Arkansas, Fayetteville, AR. Currently, he is a postdoctoral associate with Sarah Pethybridge in the Department of Plant Pathology and Plant-Microbe Biology at Cornell AgriTech, Cornell University. He is interested in biology and genetics of virulence of fungal pathogens of plants toward development of alternative management strategies of plant diseases. He is currently working with *Cercospora beticola* associated with Cercospora leaf spot (CLS) of table beet. He is interested in dissecting the influence of alternative splicing toward virulence mechanisms of *C. beticola* during pathogenicity of table beet, and developing RNAi-based approaches to control CLS and other fungal pathogens on table beet.

Sarah Pethybridge

Dr. Sarah J. Pethybridge is an associate professor in plant pathology at Cornell AgriTech, Cornell University, Geneva, NY. She is also the program leader for the Plant Pathology & Plant-Microbe Biology Section within the School of Integrative Plant Science. She received a Bachelor of Agricultural Science with First Class Honors (1995) and a Ph.D. in plant pathology (2000) from the University of Tasmania, Australia. She has worked on a broad range of crop diseases in the northern and southern hemispheres, including hops, pyrethrum, table beet, and leguminous and Allium crops. She joined Cornell University in 2014 following 18 years of experience in university, private industry, and government. Her research and extension program focuses on quantitative epidemiology and disease management serving the broad-acre vegetable industries of New York. She also teaches graduate-level epidemiology. Dr. Pethybridge's achievements have been recognized by the APS Syngenta Award in 2010, and Early Achievement Award from the College of Agriculture and Life Sciences, Cornell University, in 2018.