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From Native Plants in Central Europe to Cultivated Crops Worldwide: The Emergence of *Didymella bryoniae* as a Cucurbit Pathogen

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***Abstract.* *Didymella bryoniae* (Auersw.) Rehm [anamorph *Phoma cucurbitacearum* (Fr.) Sacc.], the plant pathogenic fungus that causes gummy stem blight and black rot on cucurbits, was first described in 1869 from *Bryonia* (bryony or wild hops) in central Europe. Today, this pathogen is found on six continents on at least 12 genera and 23 species of cucurbits. How did *D. bryoniae* progress from a pathogen of a native plant in central Europe to a worldwide threat to cucurbits cultivated in humid environments? Clues from the early discoveries of this fungus, its characteristics as a seedborne pathogen, and its broad adaptation to cucurbit hosts will provide some answers to this question.**

Early Reports of *Didymella bryoniae* and Gummy Stem Blight

Both Bernhard Auerswald and Karl Fuckel, working independently, described *Didymella bryoniae* in 1869 from specimens collected on the cucurbit *Bryonia* growing in Germany (Corlett, 1981; Robert et al., 2005). Although each mycologist assigned the fungus to a different genus, they coined the same species name "bryoniae" following the convention that the specific epithet of the fungus should be taken from the generic name of the plant host (Table 1). Because Auerswald's report was published first in 1869, he is credited with the discovery, and his name has priority according to most mycologists. Fuckel's report was not published until 1870, when volumes 23 (1869) and 24 (1870) of the journal were published together (Robert et al., 2005). Note that the genus *Didymella* was not created until 1880 by Pier Andrea Saccardo. In 1881, Heinrich Rehm transferred species *bryoniae* to *Didymella*. However, this did not prevent subsequent collectors from creating additional names for this fungus (Table 1).

The earliest collection and unambiguous report of *D. bryoniae* on a cultivated cucurbit is from *Cucumis melo* L. in Italy collected in an unknown year and described as *Didymella melonis* Pass. by Giovanni Passerini in 1885 (Corlett, 1981) (Table 1). In 1891, three collections from cultivated cucurbits were made: William Dudley found *D. bryoniae* on cucumber (*Cucumis sativus* L.) in a greenhouse on the Cornell University campus, New York (Farr and Rossman, 2010); Casimir Roumeguère found it on cucumber in France (Chiu and Walker, 1949); and Frederick Chester found it on watermelon [*Citrullus lanatus* (Thunb.) Matsum. & Nakai] in Delaware. Frederick Chester, a plant pathologist, noted that the disease had already occurred "for some years past" and resulted in "widespread financial disaster wherever it gains foothold" (Chester, 1891). All three collectors observed only pycnidia on their specimens, because they named their pathogens *Phyllosticta cucurbitacearum* Sacc., *Ascochyta cucumis* Fautr. & Roum. and *Phyllosticta citrullina* Chester with generic names of anamorphic fungi. Roumeguère and Chester created new species names that again were based on the particular host, because they apparently thought they had discovered a unique fungus. Several years later, *D. bryoniae* was found in the midwestern United States, again on cucumber, by the botanist and plant pathologist Augustine Selby (Table 1). In the first decade of the 20th century, additional collections and reports appeared from additional states in the United States and Puerto Rico (Farr and Rossman, 2010).

Note that what is assumed to be the first report of *D. bryoniae* was by Elias Fries (Table 1), one of the founders of mycology, who found a novel fungus growing on a cucurbit (genus unknown) and named it *Sphaeria cucurbitacearum* (Robert et al., 2005). The genus *Sphaeria* was used by early mycologists for fungi that produced pycnidia (asexual fruiting bodies) or perithecia (sexual fruiting bodies) (Kirk et al., 2008). Saccardo assumed that Fries found pycnidia, because he used this species epithet as the basis for his name *Phoma cucurbitacearum* (Fr.) Sacc., which is used by most scientists for the anamorph (asexual) stage of the fungus that produces pycnidia. Recently, the new name, *Stagonosporopsis cucurbitacearum* (Fr.) Aveskamp, Gruyter & Verkley, has been proposed for the anamorph based on molecular analysis and division of species of *Phoma* into numerous clades (Aveskamp et al., 2010). In reality, the distinction between asexual and sexual states of *D. bryoniae* is not terribly important biologically, because the fungus is homothallic and readily produces both fruiting bodies on a variety of hosts (Keinath, 2010).

It is interesting to note that 1) the earliest confirmed collections of *D. bryoniae* were on *Bryonia;* and 2) pseudothecia were present in each case. In contrast, the collections in the 1890s were all from cultivated cucurbits on which either only pycnidia had formed or the collectors overlooked pseudothecia. It took several more decades until the connection was made between *D. bryoniae* and its asexual state. Whether *D. bryoniae* spread from *Bryonia* to cultivated cucurbits cannot be determined, because there were no early collections of the fungus from both hosts in the same location. More likely, with the increased knowledge of basic plant pathology, gummy stem blight came to be recognized as a disease of cucurbits caused by a fungus. That this happened independently during this period can be seen from the variety of names assigned to the pathogen. Thus, most botanists, mycologists, and plant pathologists discovered *D. bryoniae* because it attracted their attention in their localities, not because they had read reports in the literature. However, Dudley and Selby, who worked at the land-grant universities Cornell and Ohio State, respectively, chose a name from the literature for their collections. Presumably, access to current literature at their places of employment influenced their identifications.

In the meantime, one of the early hosts, *B. alba* (white byrony), was introduced into the United States several times in the 19th century as an ornamental and medicinal plant. Subsequently, it escaped from cultivation and became established in the Pacific Northwest (Novak and Mack, 1995). Currently, *B. alba* is present in Washington, Idaho, Montana, and Utah; in Washington, it is considered a noxious weed. *D. bryoniae* has never been found on *B. alba* in the United States (S.J. Novak, personal communication, 19 June 1997). The most likely reason for this is that *B. alba* is found in arid environments such as southeastern Washington that are not conducive for *D. bryoniae*. In addition, the phenology of *B. alba* reduces the likelihood of contact between pathogen and host. *B. alba* is deciduous; "the stems emerge from the tuberous root in mid to late spring, and this is after the majority of the years' precipitation has fallen" (S.J. Novak, personal communication, 19 June 1997).

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Table 1. Pre-1900 collections of *Didymella bryoniae* (Auersw.) Rehm.

Yr[z]	Location	Host	Collector	Name	Reference
≈1823	Sweden?	Cucurbitaceae	E. Fries	*Sphaeria cucurbitacearum* Fr.	Robert et al., 2005
≈1869	Germany	*Bryonia cretica*	G. Rabenhorst	*Sphaerella bryoniae* Auersw.	Robert et al., 2005
≈1869	Hessen, Germany	*Bryonia* sp.	K. Fuckel	*Sphaeria bryoniae* Fuckel	Corlett, 1981
≈1870–1874	Czech Republic	*Bryonia alba*	G. Niessl	*Sphaerella bryoniae* Auersw.	Corlett, 1981
1876	England, UK	*Bryonia alba*	C. Plowright	*Sphaeria bryoniae* Fuckel	Corlett, 1981
≈1885	Italy	*Cucumis melo*	G. Passerini	*Didymella melonis* Pass.	Corlett, 1981
1891	New York (Cornell greenhouse)	*Cucumis sativus*	W. Dudley	*Phyllosticta cucurbitacearum* Sacc.	Farr and Rossman, 2010
1891	France	*Cucumis sativus*	C. Roumeguère	*Ascochyta cucumis* Fautr. & Roum.	Chiu and Walker, 1949
1891	Delaware	*Citrullus lanatus*	F. Chester	*Phyllosticta citrullina* Chester	Chester, 1891
1898	Ohio	*Cucumis sativus*	A. Selby	*Phyllosticta cucurbitacearum* Sacc.	Farr and Rossman, 2010

[z]Estimated years of collection are based on the publication date of the name assigned to the specimen.

A Seedborne Cucurbit Pathogen

D. bryoniae may be present both on and in cucurbit seed. Although it is impossible to know with certainty, two of the early reports of gummy stem blight in 1891 may have involved seedborne inoculum. According to Chiu and Walker (1949), the cucumber grown in France on which Roumeguère observed gummy stem blight was a Chinese variety, which would have been imported through seed. Dudley's observation of gummy stem blight on greenhouse cucumber also indicates that external or environmental sources of inoculum were not involved in that outbreak. One of the first reports to confirm contaminated seed as the source of inoculum for an outbreak of gummy stem blight came from England. Infested seed used for commercial crops of greenhouse cucumbers that developed gummy stem blight produced 6% diseased seedlings in a blotter test (Brown et al., 1970).

Certainly, the transition from direct seeding to transplanting cucurbits in modern agricultural systems has heightened the importance of *D. bryoniae* as a cucurbit pathogen. It consistently, albeit infrequently, appears on cucurbit seedlings in greenhouses, generally when the first true leaf appears. For example, between 1993 and 2009, gummy stem blight was found in South Carolina on greenhouse-grown watermelon and melon transplants 16 times: 11 times on seedlings grown in South Carolina and five times on seedlings grown in other states that were purchased by South Carolina growers (Keinath, 2009; Keinath, unpublished data). The typical pattern in a greenhouse flat is a dead plant that grew from a contaminated seed (primary infection) surrounded by symptomatic plants (secondary infections). In greenhouse experiments, 11% to 15% of seedlings adjacent to infected source seedlings became infected (Keinath, 1996), although higher rates of infection have been observed in commercial transplant greenhouses (Keinath, unpublished data).

van Steekelenburg (1986) demonstrated that cucumber fruit became infected after blossoms were inoculated with *D. bryoniae*. de Neergaard (1989a) traced the path of infection from conidia applied to the stigma through the style and funiculus to the ovules, which provided evidence of how cucurbit seed becomes infected with *D. bryoniae*. In a study done at The Danish Seed Health Center for Developing Countries in Copenhagen, cucurbit seeds from several countries were dissected and cultured. *D. bryoniae* was present primarily on or in the seedcoat and perisperm and occurred less frequently on the cotyledons (Lee et al., 1984). In addition, an internal fruit rot of cucumber was reported first in Japan in 1960 and then in Central America, Europe, and other locations (de Neergaard, 1989a; Kagiwata, 1970; Sitterly, 1968; van Steekelenburg, 1986). In Europe, affected fruit lacked any external symptoms. Growth of *D. bryoniae* as black mycelium also has been observed inside melon and giant pumpkin (*C. maxima*) fruits (Keinath, unpublished data). It is possible that this type of internal fruit infection could lead to seeds becoming infested with *D. bryoniae* on the outside of the seedcoat. Because fruit are externally asymptomatic, they could easily be harvested and processed to extract seed.

The use of grafted cucurbits further increases the risk of gummy stem blight development from seedborne inoculum. After grafting, plants are held at high humidity or under frequent misting to promote healing of the graft union. These environmental conditions are very favorable for development of gummy stem blight (Arny and Rowe, 1991). Recently, gummy stem blight was observed on grafted watermelon in Tunisia as cankers at the graft union that killed affected plants (Boughalleb et al., 2007). Because gummy stem blight was not observed on non-grafted plants or on leaves, it is likely that the grafted plants became infected in the greenhouse, because it is unlikely that another source of *D. bryoniae* inoculum was present in the arid North African climate.

Table 2. Cucurbit genera reported to be infected by *Didymella bryoniae*.

Genus (number of species infected)	Common name	Primary Reference for genus
Benincasa (1)	Wax gourd	Wiant, 1945
Bryonia (3)	Bryony	Auerswald, 1869, in Corlett, 1981
Citrullus (2)	Watermelon	Chester, 1891
Cucumis (3)	Cucumber; melon	Passerini, 1885, in Corlett, 1981
Cucurbita (5)	Squash, pumpkin	Grossenbacher, 1909
Cyclanthera (1)	Wild cucumber	Mendes et al., 1998, in Farr and Rossman, 2010
Lagenaria (1)	Bottle gourd	Grossenbacher, 1909
Luffa (2)	Loofah	Grossenbacher, 1909
Momordica (2)	Bitter melon	Wiant, 1945
Sechium (1)	Chayote	Wiant, 1945
Sicyos (1)	Bur-cucumber	Greene, 1953, in Farr and Rossman, 2010
Trichosanthes (1)	Snake gourd	Punithalingam and Holliday, 1972

Interactions between *D. bryoniae* and Its Cucurbit Hosts

D. bryoniae is host-specific on cucurbits (Corlett, 1981). It, like many foliar fungal pathogens, is limited to members of one host plant family. The five reports on non-cucurbit hosts in Farr and Rossman (2010) probably are misidentifications of the pathogen. Given the natural variability in severity of symptoms on inoculated plants, the host from which isolates are recovered has no consistent effect on virulence of isolates on other cucurbit species (Lee et al., 1984; Zúniga, 1999). This implies that isolates of *D. bryoniae* from wild hosts, e.g., *Bryonia* or *Sicyos angulatus*, would readily infect cultivated species. On the other hand, *D. bryoniae* is very well-adapted to cucurbits. At least 12 cucurbit genera and 23 species are hosts, i.e., can be infected and become diseased (Table 2). Nevertheless, there are consistent differences among some cucurbits. For example, summer squashes (*C. pepo*) are resistant to—or less susceptible to—gummy stem blight relative to other commonly cultivated cucurbits (Keinath, 2010; Sitterly, 1969).

D. bryoniae grows rapidly in planta. Lesion expansion has been estimated to be 0.5 cm in 12 h (Keinath, unpublished data). Epidemic progress of 6% (0.06) increase in leaf area diseased per day has been recorded on fall watermelon growing in a conducive environment without fungicide applications (Keinath, 1995). The pathogen appears to be tolerant of desiccation after infection and likely survives in planta as dormant mycelium (Chiu and Walker, 1949). It survives in dead, infected host debris for up to 2 years in semitropical climates (Keinath, 2008), which

Table 3. Comparison of geographic centers of origin for cultivated cucurbits and current distribution of *Didymella bryoniae*.

Crop	Center of origin	Reference	*D. bryoniae* occurrence[z]
Citrullus lanatus	Western, southern Africa; Egypt	Robinson and Decker-Walters, 1997	Malawi, Tanzania, South Africa
Citrullus colocynthis	Northern Africa; India	Robinson and Decker-Walters, 1997	India
Cucumis melo	India; Iran; Egypt	Robinson and Decker-Walters, 1997	India
Cucurbita pepo ssp. *ovifera*	Central and eastern United States	Pickersgill, 2007	Central and eastern United States, California
Cucurbita pepo ssp. *pepo*	Mexico	Pickersgill, 2007	Mexico
Cucurbita moschata	Mexico; Andean South America	Pickersgill, 2007	Mexico, Venezuela, Brazil
Cucurbita maxima	Bolivia; Argentina; Uruguay	Pickersgill, 2007	Venezuela, Brazil

[z]Reports of *D. bryoniae* from Farr and Rossman (2010) on any cucurbit species.

is longer than it survived in northern climates (Chiu and Walker, 1949; van Steekelenburg, 1983). Clearly, the pathogen also survives in seed (Lee et al., 1984), which provides the pathogen a selective advantage in climates where the host goes dormant and helps maintain a close host–parasite relationship (Burdon and Thrall, 2009).

D. bryoniae reproduces readily on all parts of cucurbits, including leaves, petioles, vines, stems, tendrils, pedicels, flowers, peduncles, fruits, seeds, and roots (Chester, 1891; Chiu and Walker, 1949; de Neergaard, 1989a; Keinath, 2010; Lee et al., 1984; Thinggaard, 1987). Because *D. bryoniae* is a necrotrophic fungus, fruiting bodies are found in the center or the oldest part of lesions. In general, pycnidia are formed earlier than pseudothecia, although the opposite also has been reported on cucumber (de Neergaard, 1989b). Mean number of fruiting bodies per square centimeter of leaf lesions ranged from 222 ± 58 to 579 ± 58 (Keinath, 2010). There were no differences in number of fruiting bodies per unit area on different cucurbit species. Thus, all cucurbit hosts could provide a substrate for production of airborne ascospores capable of disseminating the pathogen (Schenck, 1968). However, how far viable ascospores are capable of traveling has not been determined.

Current theory on coevolution of pathogens and host plants holds that resistance to a pathogen is most likely to occur when the pathogen is present in the plant's center of origin and exerts selection pressure on the host (see for example Burdon and Thrall, 2009). Whether susceptibility to *D. bryoniae* in cucurbits—or lack thereof—can be explained by coevolution of host and pathogen is unclear. For example, three *Cucurbita* spp. (*C. pepo*, *C. maxima*, and *C. moschata*) generally were less susceptible to foliar gummy stem blight than *Citrullus lanatus* or *Cucumis melo* with mean severities of 12%, 95%, and 94% leaf area diseased, respectively (Keinath, 2010). The overlap between prehistoric host geographic range and modern pathogen distribution is a closer match for *Cucurbita* spp. than for *Citrullus* spp. or *Cucumis melo* (Table 3; Fig. 1). In particular, subspecies of *C. pepo*, which is the least susceptible *Cucurbita* species, originated in humid areas in North America, which would have been conducive to gummy stem blight (Pickersgill, 2007; Robinson and Decker-Walters, 1997). Plants of *Cucurbita* spp. affected with gummy stem blight generally still produce an abundance of fruits, an important adaptation to colonization by a pathogen for the plant—and the domesticator.

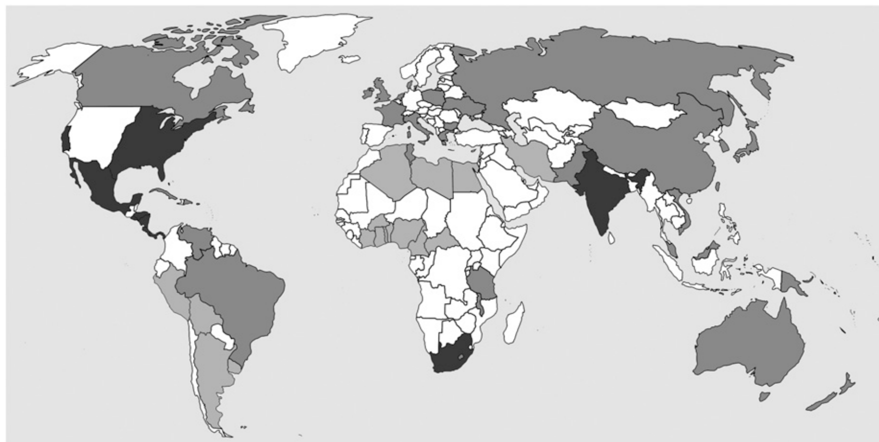

Fig. 1. Current worldwide distribution of *Didymella bryoniae* and centers of origin of *Cucurbita pepo*, *C. maxima*, *C. moschata*, *Citrullus lanatus*, and *Cucumis melo*. Dark gray = countries from which *D. bryoniae* has been reported based on Farr and Rossman (2010); Kagiwata (1970); Lee et al. (1984); Nga et al. (2010); and Punithalingam and Holliday (1972). Gray = approximate centers of origin of cucurbit hosts according to Pickersgill (2007), and Robinson and Decker-Walters (1997). See Table 3 for details of host origins. Black = centers of host origin from which *D. bryoniae* also has been reported.

Distribution of host and pathogen also may have influenced susceptibility to gummy stem blight in *Citrullus*. Fourteen *Citrullus colocynthis* accessions from Iran (seven accessions), Afghanistan (three accessions), Egypt (two accessions), Morocco (one accession), and Cyprus (one accession) were very susceptible to *D. bryoniae* (Levi et al., 2001). Because *C. colocynthis* is a desert species, and most of the accessions were collected from countries with arid climates, it is very unlikely that colocynth has been exposed to *D. bryoniae* in nature (Table 3; Fig. 1). On the other hand, citron (*C. lanatus* var. *citroides*), which originated in central Africa where *D. bryoniae* occurs, was less susceptible than both *C. colocynthis* and *C. lanatus* var. *lanatus* (Levi et al., 2001). In field evaluations, one cultivar of citron also was less susceptible to gummy stem blight than two watermelon cultivars (Keinath, 2010). It is possible, however, that citron and *Cucurbita* spp. always were inherently less susceptible to gummy stem blight than other taxa without natural selection occurring over time.

In summary, the earliest reports of *D. bryoniae* were from *Bryonia* spp. in Europe in the second half of the 19th century. By the early 20th century, *D. bryoniae* had been found on most commonly cultivated cucurbits on both sides of the Atlantic Ocean. Currently, *D. bryoniae* is part of the global movement of plant products and pathogens, because it travels from continent to continent on and in seed. Because the fungus is well adapted to cucurbits, it is able to rapidly colonize host tissue and reproduce abundantly. Thus, it is ideally suited to continue to plague cucurbits grown in humid environments.

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