

# More Than Just Plants: Botanical Gardens Are an Untapped Source of Fungal Diversity

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**Abstract.** Botanical gardens have extensive spatial databases of their plant specimens; however, the fungi occurring in them are generally unstudied. Botanical gardens, with their great plant diversity, undoubtedly harbor a wide range of symbiotic fungi, including those that are plant-pathogenic. One such group of fungi is powdery mildews (Erysiphaceae). The powdery mildews are among the most prevalent and economically important plant pathogens in the world, with an estimated 906 species in 19 genera. They are known to infect more than 10,000 species of flowering plants and although some species occur across a range of hosts, many are associated with specific plants. Powdery mildews have undergone a long and dynamic coevolution with their host plants, resulting in co-speciation. Botanical gardens provide a living laboratory in which to study these fungi, leading to a wealth of undiscovered fungal diversity. Furthermore, monitoring pathogens in botanical gardens has led to important ecological findings related to the plant sciences and plant protection. Between 2018 and 2022, a collaborative citizen science project was established with 10 botanical gardens in the United States and Mexico. A total of more than 300 powdery mildew specimens were collected on 220 different host taxa. We sequenced the entire internal transcribed spacer (ITS) and large subunit (LSU) rDNA loci and phylogenetically and morphologically analyzed these collections revealing 130 species, of which 31 are likely unknown to science. This research highlights the importance of botanical gardens as a reservoir of fungal diversity. Future research will further elucidate the coevolutionary relationship between powdery mildews and their hosts and extend the current study to evaluate other plant pathogens and fungi in botanical gardens.

Botanical gardens, by their very nature, harbor high plant diversity and are involved in plant conservation. They are considered living museums that house rare plants, common endemic species, and ornamental flora. One of the main goals of botanical gardens is to promote research to gain a better understanding and categorize the vast levels of phyto diversity on our planet. Unfortunately, one of the most common, yet least studied, groups of organisms, fungi, have gained little attention in botanical gardens. Although studies focusing on fungi in botanical gardens are minimal, in recent years, researchers worldwide have realized the potential of gardens to allow an understanding of plant–fungal interactions (Heiskanen and Valkonen, 2021; Kartika et al., 2018; Kruse et al., 2020; Rizki and Ilmi, 2021; Wanasinghe et al., 2020; Watling, 2019; Xiang et al., 2016). Botanical gardens provide a living laboratory of diverse plants in which to study plant pathogenic fungi. They can also serve as important resources for the study of non-native pathogens infecting native plants, and native pathogens that infect nonnative plant hosts (Wondafrash et al., 2021). The extensive outreach programs sponsored by botanical gardens can also provide a valuable resource to promote, expand, and contribute to scientific research.

In groups of fungi that have co-evolved with their host plants, it is inevitable that in areas of increased plant diversity, such as botanical gardens, there will be concomitant levels of increased fungal diversity. Gardens can be great resources of data to predict the host range of different fungal pathogens (Carrillo et al., 2012; Eskalen et al., 2013; Groenteman et al., 2015; Scott-Brown, 2018). Moreover, collecting and tracking fungal pathogens in botanical gardens unquestionably benefit their plant collections, as evidenced by the important research relating to ecology, the plant sciences, and plant protection that has come from monitoring plant pathogens in botanical gardens (Faraji and Karimi, 2020; Wondafrash et al., 2021). For example, alfalfa mosaic virus on peonies (Bellardi et al., 2003), potato mop top virus (Anderson et al., 2002), and bigleaf maple powdery mildew (Bradshaw et al., 2021a) were all first detected in botanical gardens.

One particular group of plant pathogens that infects a diverse range of plants and is often found in botanical gardens is powdery mildews (Erysiphaceae) (Heiskanen and Valkonen, 2021). Powdery mildews are obligate pathogens; that is, they cannot be cultivated on artificial media. The reliance of the pathogen on a living host undoubtedly led to a long and dynamic co-evolution with their host plants and co-speciation (Bradshaw et al., 2021b, 2022a; Takamatsu et al., 2010; Takamatsu, 2013). Often, species are described that are specific to a single host taxon (Bradshaw et al., 2020, 2021b). Recently, we have learned that powdery mildews are much more diverse than previously assumed (Glawe, 2004). Powdery mildews have been found on all continents except Antarctica, and they infect an estimated 9838 species of angiosperm hosts (9176 eudicots and 662 monocots) from

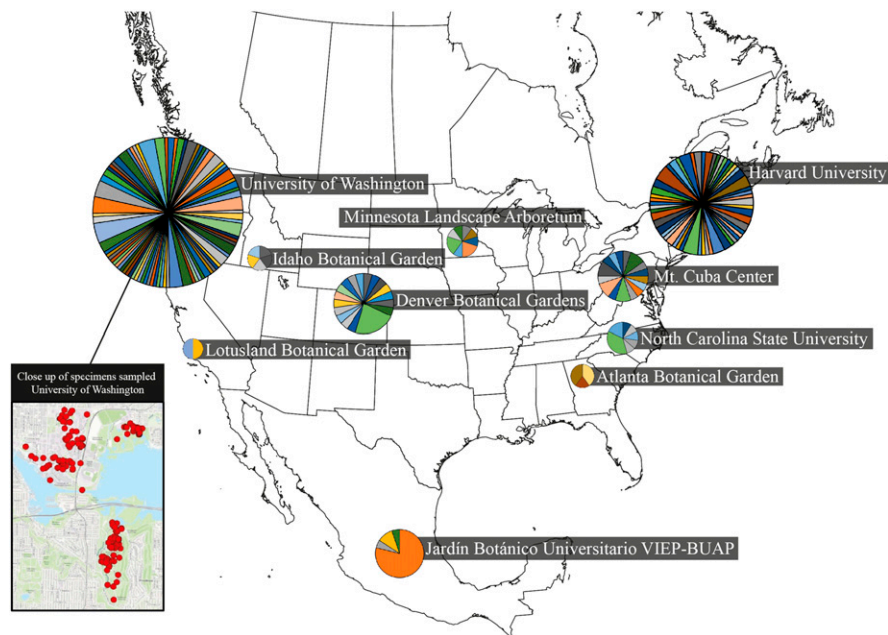


Fig. 1. Locations of powdery mildews collected from botanical gardens in North America. Different colors represent different species, and the size of the circles is proportional to the total number of species recorded from each location. The inset figure shows detailed locality of the collections from the University of Washington. The upper left corner represents the University of Washington main campus. The upper right represents the Center for Urban Horticulture. The lower right represents the Washington Park Arboretum.

more than 44 orders, 169 families, and 1617 plant genera (Amano, 1986). A total of 4.5% of angiosperm species were reported as hosts to powdery mildews (Amano, 1986). The co-evolution of powdery mildews and their hosts, their worldwide distribution, and the number of plants that collectively serve as hosts make them great target organisms for evaluation at botanical gardens.

In the present study, we created a citizen science project to collect powdery mildews from 10 botanical gardens representing different climatic regions in North America to analyze fungal diversity. A total of 130 different powdery mildew taxa were collected on 220 different host taxa; of those,  $\approx 31$  powdery

mildews were undescribed and  $\approx 45$  were first host-pathogen-locality records.

### Methods

**Collection efforts.** During the Summer and Fall of 2018 and 2019, powdery mildews were intensively collected at the University of Washington campus, which includes the main campus, the Center for Urban Horticulture, and the Washington Park Arboretum. The horticulturists at the main campus and Arboretum were notified of the project and asked to assist with collections. During the Fall of 2021, powdery mildews were collected at Harvard University, which includes the main campus and the Arnold Arboretum in Jamaica Plain. During the Spring of 2021, a volunteer program was established to collect powdery mildews from North American botanical gardens. Detailed instructions regarding sampling protocols were sent to participating botanical gardens. For example, a list of the hosts on which powdery mildew have been described across North America was compiled and shared with the collaborating botanical gardens. Contributing parties were told to sample only once from a host species. Briefly, the collection protocol was as follows: plants were examined by eye for powdery mildew colonies. If plants were showing signs of disease, then they were pressed, dried, and placed in paper bags. If the specimens were being mailed across state lines, then a shipping label was provided as well as the corresponding United States Department of Agriculture Animal and Plant Health Inspection Service permits. When the specimens arrived at the Farlow Herbarium (FH), they were placed in a  $-20^{\circ}\text{C}$  freezer for 2 weeks before analyses

in coordination with the FH Integrated Pest Management practices.

The e-mail requests were sent to 29 botanical gardens; of these, 12 responded and 10 agreed to contribute to the project. Of the 10 that agreed, two noted that “no powdery mildew was located in their gardens.” Powdery mildews from the following gardens were analyzed for the present study: the Atlanta Botanical Garden (Georgia, USA); the Denver Botanic Gardens (Colorado, USA); Harvard University (Massachusetts, USA); the Idaho Botanical Garden (Idaho, USA); Jardín Botánico Universitario VIEP-BUAP (Puebla, Mexico); Ganna Walska Lotusland (California, USA); the Minnesota Landscape Arboretum (Minnesota, USA); the Mt. Cuba Center (Delaware, USA); North Carolina State University (North Carolina, USA); and the University of Washington (Washington, USA).

**Fungal identification.** Fungal identification was accomplished by a combination of morphological and molecular analyses. Macroscopic and microscopic features of the sexual stage of the powdery mildews (chasmothecia) were studied using previously dried specimens under a stereomicroscope (Leica EZ4) and under a compound microscope (Motic B1). Images of infected leaves and close-up photographs of the chasmothecia were obtained using a Canon Eos Rebel SL2 and the Laowa 2.5–5x ultra macro. Microscopic details were photographed with a USB Moticam 2500 camera. Several chasmothecia per collection were isolated and mounted on slides with water, potassium hydroxide, Melzer’s reagent (MLZ), or Congo red (CR) to observe appendages, peridia, asci, and ascospores. Artwork for figures was created using Illustrator CS5. Sequencing was performed as

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described by Bradshaw and Tobin (2020). Briefly, DNA extractions were performed using the Chelex method (Hirata and Takamatsu, 1996; Walsh et al., 1991). Polymerase chain reaction was performed using the primers PM10/PM28R (Bradshaw and Tobin 2020) or PM10/PM2 (Cunnington et al., 2003). DNA amplicons were sent to Eurofins (Luxembourg) to be purified and directly sequenced in the forward and reverse directions using the aforementioned primers and assembled into consensus 2X sequences.

**Phylogeny.** A concatenated *GAPDH-CAMGS-ITS-LSU-RPB2* tree was constructed based on the sequences and analyses of Bradshaw and Tobin (2020) and Bradshaw et al. (2022c). Sequences were aligned and edited using MUSCLE in MEGA11: Molecular Evolutionary Genetics Analysis version 11 (Tamura et al., 2021). A GTR+G+I evolutionary model was used for phylogenetic analyses because it is the most inclusive model of evolution and includes all other evolutionary models (Abadi et al., 2019). A fixed parameter-rich model (such as GTR+G+I) can be used instead of performing a test to select the most suitable evolutionary model (Abadi et al., 2019). The phylogeny was inferred using a Bayesian analysis of the combined internal transcribed spacer (ITS) and large subunit (LSU) rDNA using a Yule tree prior (Gemhard, 2008) and a strict molecular clock with the BEAST version 1.10.4 program (Suchard et al., 2018). A single MCMC chain of 106 steps was performed, with a burn-in of 10%. Posterior probabilities were calculated from the remaining 9000 sampled trees. A maximum clade credibility tree was produced using TreeAnnotator version 1.10.4 (part of the BEAST package). Stationarity was confirmed by performing the analysis multiple times, which revealed convergence between runs. The resulting tree was visualized using FigTree version 1.3.1 (Rambaut, 2009). A maximum likelihood analysis was accomplished using raxmlGUI (Silvestro and Michalak, 2012) using the default settings with a GTR+G+I evolutionary model. Bootstrap analyses were conducted using 1000 replications (Felsenstein, 1985). Common plant families infected by each powdery mildew genus were highlighted on the tree. Evolutionary events (host diversification, herb parasitism, and arbor parasitism) were added to the tree based on a parsimonious approach. Data from the tree were acquired from Amano (1986) and Farr and Rossman (2022). Artwork for the phylogenetic tree was created using Adobe Illustrator CS5.

## Results

**Collection activities.** Between 2018 and 2019, 139 specimens were collected at the University of Washington. In the Summer/Fall of 2021, 176 specimens were collected from the Atlanta Botanical Garden (5 specimens), the Denver Botanic Gardens (22 specimens), Harvard University (82 specimens), the Idaho Botanical Garden (5 specimens), Jardín Botánico Universitario VIEP-BUAP (19 specimens), Ganna Walska Lotusland (2 specimens), the Minnesota Landscape Arboretum (10



Fig. 2. Morphology of the sexual stages (chasmothecia) of powdery mildews collected from botanical gardens highlighting their chasmothecial appendages, which are key morphological features that have been hypothesized to have co-evolved with the type of host plant (arbor vs. herbaceous). Images of the whole leaf were obtained with no magnification; then, images of the chasmothecia were obtained under a dissecting and compound microscope. (A) *Podosphaera biuncinata* on *Hamamelis* sp. (Arnold Arboretum). (B) *Erysiphe flexuosa* on *Aesculus flava* (Harvard University Campus). (C) *Erysiphe* sp. nov. on *Quercus alba* (Arnold Arboretum). (D) *Podosphaera macularis* on *Humulus lupulus* (Arnold Arboretum). (E) *Erysiphe* sp. nov. on *Alnus rubra* (Washington Park Arboretum). (F) *Phyllostictia* sp. nov. on *Oemleria cerasiformis* (Washington Park Arboretum).

specimens), the Mt. Cuba Center (20 specimens), and North Carolina State University (11 specimens). It should be noted we are only including counts of specimens that contained powdery mildews; specimens from several gardens contained no detectable powdery mildew.

A total of 315 powdery mildew specimens were evaluated using genetic and morphological data from 219 different host plant species across North America (Fig. 1, Supplementary Tables 1 and 2). These collections accounted for 130 different powdery mildew species; of these, 31 were likely undescribed species. Of the estimated 31 undescribed species collected for the current study from botanical gardens, we formally described four in previous articles (*Erysiphe viburniphila* in Bradshaw et al., 2020; *Erysiphe cornutae* and *Erysiphe coryli-americanae* in Bradshaw et al., 2021b; *Erysiphe lupini* in Bradshaw

et al., 2022b). The collections have also revealed an estimated 50 novel host–pathogen records; of these, four were formally reported by the lead author (Bradshaw et al., 2016, 2021a; Bradshaw, 2018). The remaining 27 undescribed species and  $\approx 45$  first host–pathogen records will be reported in a mycologically based project focusing on a North American Monograph of the powdery mildews.

**Phylogeny and host range analysis.** A phylogenetic tree was constructed and is presented in Fig. 3. Species of 18 out of the 19 powdery mildew genera are represented, and *Arachnopeziza* was used as an outgroup based on the analysis by Johnston et al. (2019). A maximum clade credibility tree was constructed using Bayesian analyses of the sequences by Bradshaw and Tobin (2020) and Bradshaw et al. (2022c). Thicker lines indicate higher posterior probabilities. Host range data were

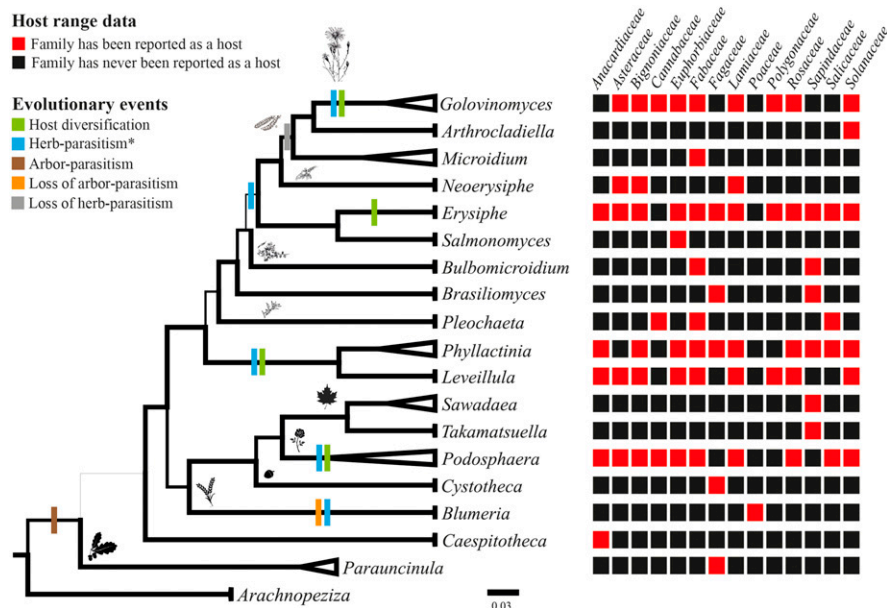


Fig. 3. Phylogenetic tree showing key evolutionary events among powdery mildew genera (upper left). The host ranges of the different genera are shown to the right. The red shading represents suitability of the host plant family to serve as a viable host. The black shading indicates that the given host family has not been reported for the associated powdery mildew genus.

included with the phylogenetic analyses. The most parsimonious explanation is that herb parasitism evolved five times throughout the powdery mildew phylogeny. Additionally, the evolution of herb parasitism is often linked to host diversification events (Fig. 3). Species of the genera *Erysiphe*, *Golovinomyces*, *Leveillula*, *Phyllactinia*, and *Podosphaera* infect the broadest range of host plants. Species within these genera can be host-specific or have an extremely wide host range. For example, *Erysiphe cornutae* and *E. coryli-americanae* are confined to single host taxa (*Corylus cornuta* and *C. americana*, respectively), whereas *Leveillula taurica* and *Golovinomyces ambrosiae* each have been reported to infect more than 50 host species (Braun and Cook, 2012; Farr and Rossman, 2022). A recent estimate of the number of described angiosperm species is 352,000 (The Plant List, 2013). Using a threshold of 4.5% to represent the number of angiosperms that are viable hosts for powdery mildew, as predicted by Amano (1986), the number of angiosperm species that are hosts to powdery mildew is 16,020. The only extensive checklist of powdery mildew hosts was performed by Amano (1986), and the 16,020 calculated here is only an estimate based on the original data of Amano (1986). The true host range of powdery mildews is unclear because new hosts are constantly added each year, as evidenced by the plant disease “first report” series and Farr and Rossman’s 2022 online database.

## Discussion

Areas of high angiosperm diversity likely contain concomitantly increased powdery mildew diversity. A prior compilation of powdery mildews in the United States, conducted in 1989, included  $\approx 70$  species (Farr et al., 1989). Our research revealed 84 species at the Washington Park Arboretum alone, and 130

species located throughout North America (Fig. 1). The diversity of powdery mildews found in this study can be attributed to the geographically widespread sampling effort occurring on a range of endemic and introduced host plants as well as the host specificity of these phytopathogens resulting from host–parasite co-evolution.

Evidence of the co-evolution of powdery mildews with their host plants has been shown genetically and morphologically (Bradshaw et al., 2022a; Shirouzu et al., 2022; Takamatsu et al., 2010; Takamatsu et al., 2013). Phylogenetic analyses have revealed associations between powdery mildew genera with certain plant families (Fig. 3). For example, *Podosphaera* has a strong co-evolution with plants in the Rosaceae family, and *Golovinomyces* has a strong co-evolution with plants in the Asteraceae family (Bradshaw et al., 2022a; Takamatsu et al., 2010; Takamatsu et al., 2013). Moreover, morphological features of host plants have been hypothesized to have co-evolved with aspects of the powdery mildew sexual stage (Shirouzu et al., 2022). For example, chasmothecial appendages with circinate or branched apices (Fig. 2B and E, respectively) tend to be found on powdery mildews that infect deciduous trees because these appendages are used to attach to secondary substrates such as bark and adjacent plants (Gadoury and Pearson, 1988; Grove and Boal, 1991). Mycelium-like appendages (Fig. 2D) usually infect herbaceous plants because these appendages are more likely to remain on the leaves of the host and infect plant material that emerge in the following spring (Gadoury et al., 2010).

Although powdery mildews are globally recognized as relatively common plant pathogens, taxonomic and phylogenetic analyses are

often lacking; in-depth studies (usually in the form of regional monographs) have been conducted only in China, Japan, Europe, and the Middle East (Braun, 1995; Chen et al., 1987; Khodaparast and Abbasi, 2009; Sato and Eto, 2014; Shin, 2000; Takamatsu, 2012). The most host plants have been observed in Asia, Europe, and North America (Amano, 1986). Continued explorations of botanical gardens in understudied regions are likely to increase the known powdery mildew host range and reveal new hot spots of fungal diversity. It should be noted that the possible hosts predicted by this study (16,020) is a conservative underestimate based on the estimates of Amano (1986), who stated that “the true host range of powdery mildew fungi must be substantially wider than that indicated in this book.” Recently, Heiskanen and Valkonen (2021) collected 94 plants infected with powdery mildews from a botanical garden in Southern Finland and observed 28 species. Heiskanen and Valkonen (2021) concluded, as have we, that botanical gardens, with their diversity of native and non-native plants, maintain both genetic diversity of plants and their pathogens. They are also a perfect venue for elucidating fungal plant pathogenic host ranges. This research highlights the value of botanical gardens as a reservoir of fungal diversity and as a resource for understanding the evolutionary relationships between powdery mildews and their host plants.

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Supplementary Table 2. (Continued)

**Plant hosts of powdery mildews collected**

*Geranium oreganum*  
*Geranium viscosissimum*  
*Geum macrophyllum*  
*Geum* sp.  
*Grindelia integrifolia*  
*Hamamelis virginiana*  
*Hebe* sp.  
*Hedera hibernica*  
*Helianthus annuus*  
*Helianthus mollis*  
*Helianthus tuberosus*  
*Heuchera* sp.  
*Humulus lupulus* 'Canadian Red Vine'  
*Hydrangea macrophylla*  
*Hydrophyllum canadense*  
*Hypericum perforatum*  
*Ilex verticillata*  
*Juglans ailantifolia*  
*Juglans nigra*  
*Lactuca serriola*  
*Lagenaria siceraria*  
*Lagerstroemia indica* 'Hardy Lavender'  
*Lamium purpureum*  
*Lathyrus latifolius*  
*Leuzea carthamoides*  
*Liatris spicata* 'Floristan Weiss'  
*Liriodendron tulipifera*  
*Lonicera ciliosa*  
*Lonicera involucrata*  
*Lonicera japonica*  
*Lupinus albicaulis*  
*Lupinus latifolius*  
*Lupinus lepidus*  
*Lupinus polyphyllus*  
*Lupinus rivularis*  
*Lycium chinense*  
*Magnolia acuminata*  
*Magnolia globosa*  
*Magnolia liliiflora*  
*Magnolia macrophylla*  
*Magnolia stellata*  
*Magnolia wilsonii*  
*Magnolia × soulangeana*  
*Malus fusca*  
*Malus pumila*  
*Malus sylvestris*  
*Melica subulata*  
*Melissa officinalis*  
*Monarda fistulosa*  
*Nandina domestica*  
*Nelumbo nucifera*  
*Oemleria cerasiflorus*  
*Oenothera biennis*  
*Osmorhiza claytonii*  
*Oxalis* sp.  
*Paeonia lactiflora*  
*Parthenocissus quinquefolia*  
*Penstemon serrulatus*  
*Phacelia bipinnatifida*  
*Phlox* sp.  
*Physocarpus opulifolius*  
*Plantago major*  
*Platanus × hispanica*  
*Platanus occidentalis*  
*Platanus orientalis*  
*Poaceae*  
*Populus balsamifera*  
*Prunus* sp.  
*Quercus cerris*  
*Quercus agrifolia*  
*Quercus gambelii*  
*Quercus garryana*  
*Quercus glaucooides*

(Continued)

Supplementary Table 2. (Continued)

**Plant hosts of powdery mildews collected**

*Quercus glaucooides* × *Q. microphylla*  
*Quercus insgnis*  
*Quercus invaginata*  
*Quercus laceyi*  
*Quercus liebmannii*  
*Quercus liebmannii* × *Quercus microphylla*  
*Quercus aff. miquihuanensis*  
*Quercus muehlenbergii*  
*Quercus nigra*  
*Quercus obtusata*  
*Quercus pacifica*  
*Quercus prinoides*  
*Quercus robur*  
*Quercus rubra*  
*Quercus sebifera*  
*Ranunculus repens*  
*Ratibida columnifera*  
*Rhododendron occidentale*  
*Rhododendron* sp.  
*Rhus aromatica*  
*Rhus glabra*  
*Rhus michauxii*  
*Rhus typhina*  
*Ribes bracteosum*  
*Ribes lacustre*  
*Ribes sanguineum*  
*Rosa gallica*  
*Rosa gymnocarpa*  
*Rosa nutkana*  
*Rosa pisocarpa*  
*Rosa woodsii*  
*Rubus armeniacus*  
*Rubus leucodermis*  
*Rubus parviflorus*  
*Rubus pentalobus*  
*Rubus spectabilis*  
*Rubus ursinus*  
*Rudbeckia fulgida*  
*Salix* sp.  
*Sambucus* sp.  
*Sarracenia* sp.  
*Sedum* sp.  
*Sidalcea hendersonii*  
*Solanum lycopersicum*  
*Solidago* sp.  
*Sonchus oleraceus*  
*Spiraea* spp.  
*Stachys aspera*  
*Stylophorum diphyllum*  
*Symphoricarpos albus*  
*Symphytotrichum georgianum*  
*Symphytotrichum novi-belgii*  
*Symphytotrichum patens*  
*Syringa vulgaris*  
*Taraxacum officinale*  
*Tellima grandiflora*  
*Thalictrum* sp.  
*Tiarella* 'Spring Symphony'  
*Tolmiea menziesii*  
*Ulmus americana*  
*Ulmus pumila*  
*Ulmus* sp.  
*Uvularia grandiflora*  
*Vaccinium corymbosum* 'Earl Blue'  
*Vaccinium parvifolium*  
*Verbena bonariensis*  
*Verbesina alternifolia*  
*Vernonia fasciculata*  
*Vernonia glauca*  
*Veronica spicata* 'Glory'  
*Viburnum edule*  
*Viburnum lentago*  
*Viburnum opulus*

(Continued)

Supplementary Table 2. (Continued)

**Plant hosts of powdery mildews collected**

*Viburnum tinus*  
*Vitis* sp.  
*Zinnia elegans*