

REVIEW

Hydrangea Diseases in Japan

Susumu NAGASHIMA^{1,2} and Motoaki TOJO^{2*}

¹Shimane Agricultural Technology Center, Izumo, Japan

²Graduate School of Agriculture, Osaka Metropolitan University, Sakai, Japan

Abstract

The genus *Hydrangea* comprises 70-80 species, some of which have economic importance as flowering plants. Japan has at least 71 hydrangea diseases and approximately one-third of the world's recorded hydrangea diseases. A large number of hydrangea diseases in Japan are known primarily due to the long history of disease studies since 1892, and the pathogen diversity caused by Japan's high humidity and temperature ranges. Recently, new diseases have been found in several high-value cultivars that have been grown as potted plants in greenhouses in Japan. Such growing environments with high humidity and temperature may have enhanced development of the new diseases. An overall risk assessment is needed to ensure proper management of both old and new diseases of hydrangeas. This review lists all known hydrangea diseases recorded in Japan, compared them to global records, and reveals the diversity as well as the uniqueness of the diseases in the country. In addition, eight diseases, i.e., ring spot, bacterial leaf spot, stem and root rot, powdery mildew, gray mold, leaf spot/stem rot, anthracnose, and leaf spot, which are currently problematic in Shimane Prefecture, Japan, are addressed based on four features: 1) symptoms, 2) distribution, 3) occurrence, and 4) control.

Discipline: Agricultural Environment

Additional key words: disease control, distribution, pathogen species, occurrences

Introduction

The genus *Hydrangea* includes 70-80 species of flowering plants that originate in Asia and the Americas (Slade 2020, WCVP 2022). Common hydrangea [*Hydrangea macrophylla* (Thunb.) Ser.], which is native to Japan, is the most popular species of the genus worldwide (Hotta et al. 1989, Waki et al. 2018). Japan has a long history of hydrangea cultivation. The oldest record of hydrangea in the country was described in Man'yōshū, a Japanese classic anthology written in the 8th century (Osawa & Arai 2016). Hydrangea had been widely planted in gardens in the Kamakura period (1185-1333), and its cultivation and propagation methods were published in gardening books during the Edo period (1603-1868) (Osawa & Arai 2016). Soon thereafter, Japanese hydrangeas were introduced into European countries and the United States (Kawarada et al. 2010). The new

hydrangea cultivars bred in these countries were reintroduced into Japan in the Taisho period. Because these new cultivars had large and various colored flowers, domestic demand in Japan for them increased especially in the latter half of the 20th century (Kawarada et al. 2010). Recently, *H. macrophylla* and its related hydrangeas are economically the most important; for example, their sales reached 1,773 million yen (2.284 million potted plants) in 2019 in Japan (The Japanese Flower Auction Association 2020). Some high-value cultivars of *H. macrophylla* that have double flowers, unique color, and dwarf nature have recently been bred and contributed to increasing farmers' profits (Ishii 2019).

Japan has one of the oldest histories of hydrangea diseases since *Pucciniastrum hydrangeae* was recorded on *H. paniculata* in 1892 (Tsukiboshi et al. 2007). Hydrangeas, as well as other ornamental plants, have

*Corresponding author: tojo@omu.ac.jp

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suffered from many pathogens (NARO Genebank 2022a). Shimane Prefecture is one of the major hydrangea cultivation areas in Japan. Since hydrangea diseases were first recorded in the area in the 1950s (Yamamoto & Yasumori 1960), the disease problems continue to date (Nagashima et al. 2021a, b). Comprehensive documentation focusing on the hydrangea diseases in Shimane Prefecture is not only important to the local economies but also notable for considering the significance of the diseases throughout Japan and other countries. However, hydrangea diseases in Japan, including Shimane Prefecture, have not been summarized, although hydrangea diseases, mainly in North America, have recently been reviewed (Li et al. 2016, Baysal-Gurel et al. 2016). To provide practical information on hydrangea diseases in Japan, this paper lists all previous records of hydrangea diseases, including insufficient records, in Japan (Table 1). We also focused on the eight diseases that are problematic in Shimane Prefecture on 1) symptoms, 2) distribution, 3) occurrence, and 4) control. Their application scopes are also highlighted. In this review, characteristic features are elucidated for hydrangea diseases in Japan.

Ring spot (pathogen: *Hydrangea ringspot virus*)

1. Symptoms

Chlorotic or reddish-brown spots or rings (Fig. 1 a, b), distorted, crinkled, and rolled leaves. Other symptoms are dwarfing and a reduction in the number of florets per inflorescence. Symptoms may depend on the cultivar and environmental conditions. Hydrangeas infected with this virus are often symptomless.

2. Distribution

Hydrangea ringspot virus is distributed worldwide (Table 1). The virus has often been recorded in Japan although it has not been proposed as the disease name in the Japanese plant disease index (NARO Genebank 2022a). Obata and Yamamoto (1968) detected the virus in the imported hydrangea cuttings from the Netherlands. The natural occurrence of the virus with typical ringspot symptoms on the leaves was first reported in Japan by Yusa et al. (2016). The virus was also detected in Shimane Prefecture by molecular biological techniques from hydrangea leaves having symptoms of chlorotic or reddish-brown spots or rings (Fig. 1 a, b).

3. Occurrence

This virus is transmitted by sap blades but not seed transmission (Brierley & Lorentz 1957). No vector-borne infection has been reported (Koenig 1973). Therefore, the

use of healthy mother plants for propagation is the primary way to control this disease.

4. Control

Sterilization of pruning tools can reduce the risk of viral transmission. Suspicious symptomatic plants should be immediately removed to prevent further development of the disease. The virus infections can be diagnosed by detecting antigens with the DAS-ELISA and by amplification of the viral RNA with RT-PCR (Tóth et al. 2012).

Bacterial leaf spot (pathogen: *Acidovorax valerianellae*)

1. Symptoms

Symptoms appear as large water-soaked lesions (Fig. 1 c) and black discolorations of hydropores on lower leaves (Fig. 1 d), which emerge as small spots together with distortion on upper leaves (Fig. 1 e).

2. Distribution

The disease was first reported by Takikawa et al. (2008). Since then, it has been recorded in Gunma (Ikeda et al. 2009) and Shimane Prefectures (Fig. 1 c, d, e), Japan. Due to the pathogen has a worldwide distribution (Grondeau et al. 2007, Han et al. 2012, Takikawa et al. 2008), and causing severe disease (Ikeda et al. 2009), hydrangeas have the potential to be damaged by this disease worldwide.

3. Occurrence

The occurrence of the disease is limited to potted hydrangeas during forced culture after dormant periods of the plants. This pathogen bacterium, *A. valerianellae*, can cause symptoms in a wide variety of hydrangeas and other plants, including melon (*Cucumis melo*), kiwifruit (*Actinidia deliciosa*), tea plant (*Camellia sinensis*), and sesame (*Sesamum indicum*) (Ikeda et al. 2009, NARO Genebank 2022a). *A. valerianellae* was originally described as a pathogen of common cornsalad (Gardan et al. 2003). A high incidence of *in vitro* bacterial contamination has been detected in meristem tip explants of hydrangea (Cassells & Tahmatsidou 1996); therefore, this pathogen can survive in hydrangea flower buds during a dormant period (Ikeda & Furuya 2020).

4. Control

The optimum temperature for disease development is 20°C-25°C, and the disease occurs after plants have been exposed to saturated humidity for >1 day at 20°C-25°C (Ikeda & Furuya 2012). As *A. valerianellae* is

Table 1. Pathogens of *Hydrangea* spp. recorded in Japan

Pathogens including putative	Host name ^{a)} (Locations other than Japan)	References ^{b)}
Virus		
<i>Cucumber mosaic virus</i>	Hma (Italy, Korea)	1, 29, 56
<i>Hydrangea ringspot virus</i>	Hma, Hse (worldwide)	2, 3, 4, 78
Phytoplasma		
' <i>Candidatus Phytoplasma asteris</i> '	Hma, Hsp (Belgium, Italy)	5, 6
' <i>Candidatus Phytoplasma japonicum</i> '	Hma, Hse	7, 8
Bacteria		
<i>Acidovorax valerianellae</i>	Hma, Hsp	9, 10
<i>Pseudomonas syringae</i>	Hsp	11
<i>Ralstonia solanacearum</i>	Hma, Hpa, Hqu (USA)	12, 13
Oomycetes		
<i>Globisporangium</i> sp.	Hma	14
<i>G. spinosum</i>	Hma	14
<i>G. splendens</i>	Hma	14
<i>Phytophthora hedraiaandra</i>	Hma	15
<i>Pythium myriotylum</i>	Hma	14
Fungi		
<i>Aecidium</i> sp.	Hlob, Hmame (Philippines)	16, 22
<i>A. hydrangeae</i>	Hda, Hhi, Hlon, Hma, Hst, Hsp (China)	16, 17, 18, 102
<i>A. hydrangeae-paniculatae</i> (= <i>Puccinia glyceriae</i>)	Hpa	17, 19, 20, 90
<i>A. hydrangiicola</i> (= <i>Puccinia suzutaekae</i>)	Han, Hanp, Hhi, Hin, Hlof, Hlon, Hmat, Hro, Hum (China, Taiwan)	16, 17, 21, 90
<i>Amphisphaeria</i> sp.	Hpa	23
<i>Armillaria mellea</i>	Hma, Hqu, Hsp (Canada, USA)	16, 24, 25, 26
<i>Auricularia polytricha</i>	Hpa	27
<i>Botrytis cinerea</i>	Har, Hhos, Hma, Hmao, Hpa, Hpe, Hsp (worldwide)	14, 16, 28, 30, 31, 32
<i>Cercospora</i> sp.	Har, Hma, Hse, Hsp (Iran, USA)	16, 44, 45
<i>C. hydrangeae</i>	Hanp, Harg, Hhoa, Hhos, Hma, Hmaa, Hmao, Hpa, Hsea, Hsp (worldwide)	16, 24, 32, 33, 34, 35, 36, 37, 38
<i>C. hydrangeana</i>	Hanp, Hhos, Hsp, Hma, Hmao (Malawi, Malaya, Nyasaland, Taiwan, USA)	16, 39, 40, 41, 42
<i>C. kyotensis</i>	Hset	43
<i>C. obtogens</i> (= <i>Pseudocercospora obtogens</i>)	Hma (China)	16
<i>C. yakushimensis</i> (= <i>Pseudocercospora yakushimensis</i>)	Hkag	46
<i>Colletotrichum destructivum</i>	Hma	47
<i>C. hydrangeae</i> (= <i>Glomerella cingulata</i>)	Hch, Hma, Hmao, Hsc (China, Taiwan)	16, 48, 49, 60
<i>Corynespora cassiicola</i>	Hhos, Hma, Hsp (Burma, China, Hong Kong, Malaya, USA)	16, 50, 51, 52, 53, 54
<i>Cristulariella pyramidalis</i> (= <i>Cristulariella moricola</i>)	Hpe	55
<i>Cylindrobasidium argenteum</i>	Hin	16
<i>Diaporthe detrusa</i>	Hpa	57
<i>D. eres</i>	Har, Hpa (USA)	16, 57
<i>Diplocladium hydrangeae</i>	Hopa	19
<i>Discosia</i> sp.	Hlu	38
<i>D. artocreas</i>	Hsc	19
<i>Erysiphe hydrangeae</i>	Hpa (China)	58, 59
<i>E. schizophragmatis</i>	Hpe	58,
<i>Glomerella cingulata</i> (= <i>Colletotrichum gloeosporioides</i>)	Hma, Hmaa, Hmn, Hmao, Hpe, Hsc, Hsp (Brunei Darussalam, Cuba, Hong Kong, USA)	16, 49, 60
<i>Haploporus odoris</i>	Hpa	61, 62
<i>Metasphaeria hydrangeae</i>	Hmao	49
<i>Microporus vernicipes</i>	Hpa	27
<i>Microsphaera</i> sp.	Hmao, Hmame, Hpa	65, 66
<i>M.alni</i>	Hma, Hpa (USA)	63, 64
<i>Mycena brevicapitata</i>	Hin	67
<i>M. haematopoda</i>	Hpa	27
<i>Mycosphaeraella hydrangiae</i>	Hhi	68
<i>Oidium</i> sp.	Hhos, Hma, Hmn, Hmame, Hmao, Hmat, Hsp (worldwide)	16, 32, 36, 66, 72, 73, 74, 75
<i>O. hortensiae</i> (= <i>Pseudoidium hortensiae</i>)	Har, Hhoa, Hhos, Hin, Hma, Hse, Hsej, Hset, Hmn, Hmaa, Hmame, Hse, Hop, Hpa, Hsp, Hxa (worldwide)	16, 69, 70, 71
<i>Pestalotiopsis adusta</i>	Hlu	24
<i>Phoma</i> sp.	Hma (USA)	16, 79
<i>P. exigua</i> (= <i>Boeremia exigua</i>)	Hma, Hqu (Italy, USA)	16, 76, 77
<i>Phyllosticta capitalensis</i>	Hqu	80
<i>P. hydrangeae</i> (= <i>Boeremia exigua</i>)	Har, Hhi, Hhoa, Hma, Hmama, Hmao, Hpa, Hpe, Hsp (worldwide)	16, 38, 81
<i>P. micrococciata</i>	Hsea	82
<i>Porodaedalea lonicerina</i>	Hpa	27
<i>Pseudoidium hortensiae</i>	Hma, Hsea, Hsem, Hsp (Korea, Norway, Thailand)	58, 83, 84, 85
<i>Puccinia</i> sp.	Hpa	87
<i>P. glyceriae</i>	Hpa, Hsea (Korea)	16, 86
<i>P. suzutaekae</i>	Han, Hhi, Hlof, Hlu, Hmn, Hmaa, Hmat, Hsc, Hsp (Taiwan)	16, 88, 89, 90
<i>Pucciniastrum hydrangeae</i>	Hpa, Hpe (USA)	16, 102
<i>P. hydrangeae-petiolaridis</i>	Hano, Hhe, Hkak, Hpa, Hpe, Hro, Hsp (China, Himalaya, Taiwan, USSR)	16, 21, 48, 89, 91, 93, 94, 95
<i>P. hydrangeae-petiolaris</i>	Hpe, Hsp (China, Nepal, USSR)	18, 96
<i>Rhizina undulata</i>	Hpa	97
<i>Rhizoctonia solani</i>	Hma, Hsp (Rhodesia, USA)	16, 32, 98
<i>Rosellinia necatrix</i>	Hin, Hma, Hpa	99
<i>Sphaeloma</i> sp.	Hse	100
<i>Stereum ostrea</i>	Hpe	101
<i>Trametes versicolor</i>	Hpa	27
<i>Uncinula hydrangeae</i> (= <i>Erysiphe hydrangeae</i>)	Hpa (China)	58, 59
<i>Zygothia jamaicensis</i>	Hpa	92

^{a)} Hma: *Hydrangea macrophylla*, Hmama: *H. macrophylla* var. *macrophylla*, Hmao: *H. macrophylla* var. *otakusa*, Hmat: *H. macrophylla* var. *thunbergii*, Hmame: *H. macrophylla* var. *megacarpa*, Hmaa: *H. macrophylla* var. *acuminata*, Hmn: *H. macrophylla* f. *normalis*, Hsp: *Hydrangea* sp., Hse: *H. serrata*, Hsca: *H. serrata* var. / f. *acuminata*, Hsem: *H. serrata* var. *megacarpa*, Hset: *H. serrata* var. *thunbergii*, Hsej: *H. serrata* f. *japonica*, Hqu: *H. quercifolia*, Hpa: *H. paniculata*, Hpaif: *H. paniculata* var. *floribunda*, Hpc: *H. petiolaris*, Hda: *H. davidii*, Hhi: *H. hirta*, Hlon: *H. longipes*, Hst: *H. strigosa*, Han: *H. angustipetala*, Hanp: *H. angustisepala*, Hin: *H. involucrata*, Hlof: *H. longifolia*, Hro: *H. rosthornii*, Hum: *H. umbellata*, Hlob: *H. lobbia*, Hano: *H. anomala*, Hhoa: *H. hortensia*, Hhos: *H. hortensis*, Hch: *H. chinensis*, Hop: *H. opuloides*, Hopa: *H. opuloides* var. *angustata*, Har: *H. arborescens*, Hard: *H. arborescens* subsp. *discolor*, Hkag: *H. kawagoeana*, Hsc: *H. scandens*, Hlu: *H. luteo-venosa*, Hhe: *H. heteromalla*, Hkak: *H. kawakamii*, Hxa: *H. xanthoneura*

^{b)} 1: Tamura & Komuro (1967), 2: Chiko & Godkin (1986), 3: Briery & Lorentz (1957), 4: Yusa et al. (2016), 5: Bertaccini et al. (1992), 6: Takinami et al. (2013), 7: Kanehira et al. (1996), 8: Sawaynagi et al. (1999), 9: Takikawa et al. (2008), 10: Ikeda et al. (2009), 11: Shirata et al. (1984), 12: Ji et al. (2007), 13: Kusumoto et al. (2009), 14: Nagashima et al. (2021a, b), 15: Yosifita et al. (2020), 16: USDA ARS (2022), 17: Yasuda (1911), 18: Zhang et al. (1997), 19: Togashi & Onuma (1934), 20: Yoshinaga (1905), 21: Zhuang (1983), 22: Harada & Fujita (1998), 23: Miura (1957), 24: Kobayashi (1977a, b), 25: Raabe (1965), 26: Raabe (1967), 27: Endo (1964), 28: Arai (1996), 29: Bang et al. (2001), 30: Riviera et al. (2004), 31: Garibaldi et al. (2017), 32: Whiteside (1966), 33: Horie & Kobayashi (1984), 34: Shin & Braum (2000), 35: Gautam et al. (2020), 36: Williams & Liu (1976), 37: Yamamoto & Maeda (1960), 38: Yamamoto & Yasumori (1960), 39: Katsuki (1949), 40: Thompson & Johnston (1953), 41: Wiehe (1953), 42: Yamamoto (1936), 43: Yoshikawa & Yokoyama (1992), 44: Bakhshi et al. (2015), 45: Groenewald et al. (2013), 46: Togashi & Katsuki (1952), 47: Moriwaki et al. (2003), 48: Sawada (1943a, b), 49: Tsukamoto & Katsuki (1959), 50: Johnston (1960), 51: Kasuyama & Idei (1987), 52: Sobers (1966), 53: Thaug (2008), 54: Zhu et al. (2020), 55: Yokoyama & Tsubaki (1974), 56: Bertaccini et al. (2015), 57: Kobayashi (1970), 58: Braum & Cook (2012), 59: Nomura & Tanda (1985), 60: Nakamura (1970), 61: Chiba & Teramoto (1952), 62: Aoshima & Kobayashi (1983), 63: Hirata (1956), 64: Yarwood & Gardner (1970), 65: Seki & Hirata (1961), 66: Honma & Hirata (1968), 67: Takahashi (2000), 68: Hara (1918), 69: Park et al. (2012), 70: Tanda (1997), 71: Tanda (1999), 72: Orioux & Felix (1968), 73: Hirata & Wada (1973), 74: Horie et al. (1997), 75: Tanda et al. (1973), 76: Garibaldi et al. (2006), 77: Takano (1994), 78: Koening (1973), 79: Ikeda et al. (2010), 80: Motohashi et al. (2009), 81: Hara (1930), 82: Miura (1962), 83: Cho et al. (2018), 84: Meeboon & Takamatsu (2015), 85: Wanarsi et al. (2020), 86: Okane & Kakishima (1991), 87: Ogawa (1996), 88: Kakishima & Sato (1981), 89: Hiratsuka & Chen (1991), 90: Matsuura (1904), 91: Hiratsuka (1927), 92: Nasu & Kinosh (1987), 93: Guo (1989), 94: Zhuang & Wei (1994), 95: Zhuang (2005), 96: Liang et al. (2006), 97: Sato et al. (1974), 98: Fujii & Murakami (1974), 99: Ito & Nakamura (1984), 100: Ono et al. (2010), 101: Kamei (1958), 102: Tsukiboshi et al. (2007)

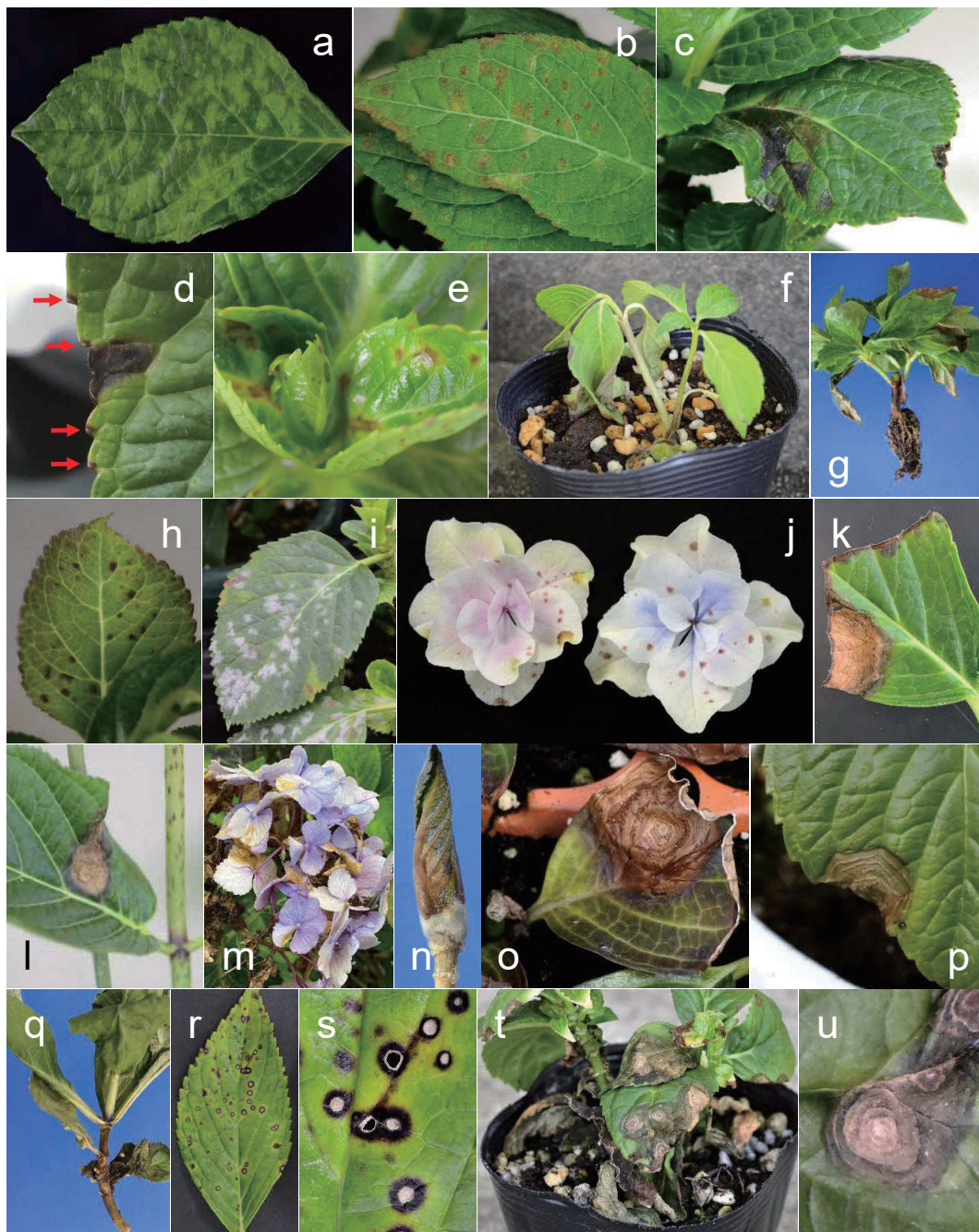


Fig. 1. Symptoms of hydrangea diseases

a-b. *Hydrangea ringspot virus*, **c-e.** Bacterial leaf spot caused by *Acidovorax valerianellae*, **f-g.** Stem and root rot caused by *Pythium myriotylum* and *Globisporangium* spp., **h-j.** Powdery mildew caused by *Oidium* sp., **k-n.** Gray mold caused by *Botrytis cinerea*, **o-q.** Leaf spot caused by *Phoma* sp., **r-s.** Anthracnose caused by *Glomerella cingulata*, **t-u.** Leaf spot caused by *Corynespora cassiicola*.

a soil-borne pathogen in cornsalad, it may also be a soil-borne pathogen in hydrangea (Ikeda & Furuya 2020). Therefore, to prevent the disease, potted hydrangeas should avoid natural field soil and high humidity by growing on benches in the field and greenhouses. It is effective to control the disease by spraying copper 8-quinolonolate (Liu et al. 1994) three times at

2-week intervals in autumn when flower buds begin to form (Ikeda et al. 2022). This fungicide has been registered in Japan.

Stem and root rot (pathogens: *Pythium myriotylum*, *Globisporangium splendens*, *G. spinosum*, *Globisporangium* sp.)

1. Symptoms

The typical symptoms are water-soaked and dark-brown lesions that initially appear at the base of the stems of young plants. These lesions gradually enlarge, and discoloration (Fig. 1 f) and abscission of leaves are followed by plant death. Roots of damaged plants show rot and appear water-soaked (Fig. 1 g), and hyphal swellings (Fig. 2 a, c, e) and oogonia (Fig. 2 b, d) are formed in the cells of the roots. Older potted plants, 3-7 months old, also have dark-brown lesions on the base of the stems and roots. Some have chlorotic leaves, stunted growth, and wilt.

2. Distribution

Most of the pathogens are distributed worldwide with a wide host range (van der Plaats-Niterink 1981). Although their records on hydrangea have only been known in Shimane Prefecture, Japan (Table 1), there is the potential to develop these diseases in other countries if the contaminated soil is used for potted growth.

3. Occurrence

Stem and root rot has been recently recorded on hydrangea in Japan (Nagashima et al. 2021a). Increased cultivation of susceptible cultivars may be the main contributing factor to the occurrence of the disease. The cultivar “Mangekyo” is the most susceptible to all these pathogens (Nagashima et al. 2021a). The pathogens can survive in soil particles and growing media on materials such as greenhouse floors and used pots (van der Plaats-Niterink 1981). Younger hydrangea plants are particularly susceptible to the disease (Nagashima & Tojo 2021).

4. Control

Pot soil needs to be disinfected by heat treatment or soil disinfectant. Soil disinfestation with a mixture of metalaxyl-M and azoxystrobin (Uniform®) before transplanting is effective in preventing all four pathogens of the disease (Nagashima et al. 2020). This fungicide is registered for the protection of potted hydrangeas against stem and root rot disease in Japan. Growers should also use clean pots and pot trays. Disinfection of the plant growth materials can be done using sodium hypochlorite solutions at a total free chlorine concentration of 14 mg L⁻¹ for 10 min. (Cayanan et al. 2009).

Powdery mildew (pathogen: *Erysiphe hydrangeae*, *Microsphaera alni*, *Microsphaera* sp., *Oidium* sp. and *Pseudoidium hortensiae*)

1. Symptoms

Pathogens of powdery mildew are several species of the genera, including *Erysiphe*, *Microsphaera*, *Oidium*, and *Pseudoidium* (NARO Genebank 2022a). The disease caused by *Oidium* sp. is commonly found in Shimane Prefecture. This occurs on leaves (Fig. 1 h, i), petals (sepals) (Fig. 1 j), and young stems. The first sign is small white powdery spots on leaves that rapidly spread and cover the tissue. Infected tissues turn reddish purple (Fig. 1 h, j). The damaged leaves often become distorted. The severely affected leaves defoliate early.

2. Distribution

Three species, *Erysiphe hydrangeae*, *Microsphaera alni*, and *Microsphaera* sp., have limited distribution in the world (Table 1). In Japan, these species are distributed as follows: *Erysiphe hydrangeae*; Tokyo, Hokkaido, Yamanashi, Fukushima, Nagano, Aomori, Mie, Niigata, and Tochigi Prefectures (Nomura & Tanda 1985), *Microsphaera alni*; Ibaraki Prefecture (Hirata 1956), and *Microsphaera* sp; Niigata Prefecture (Seki & Hirata 1961). In contrast, *Oidium* sp. and *Pseudoidium hortensiae* are distributed worldwide (Table 1). In Japan, these species are distributed as follows: *Oidium* sp.; Hokkaido (Narita 1998), Tokyo (Horie et al. 1997), Niigata (Hirata & Wada 1973) and Shimane Prefectures (Fig. 1 h, i, j; Fig. 2 f, g, h), *Pseudoidium hortensiae*; Tokyo and Niigata Prefectures (Meeboon & Takamatsu 2015, Tanda 1999).

3. Occurrence

Oidium sp. may survive on stems in winter (Horie et al. 2020). Conidia (Fig. 2 h) formed on the conidiophores (Fig. 2 f, g) are spread by airflow and infect healthy leaves. Powdery mildew outbreaks in Japan are common in the rainy season (June to July) and fall (September to November).

4. Control

Use of healthy cuttings and resistant cultivars are effective ways to control the disease. In addition, growers should not grow many cultivars in the same greenhouse because susceptible cultivars can be a source of infection. Spraying fungicides before infection or disease development is effective.

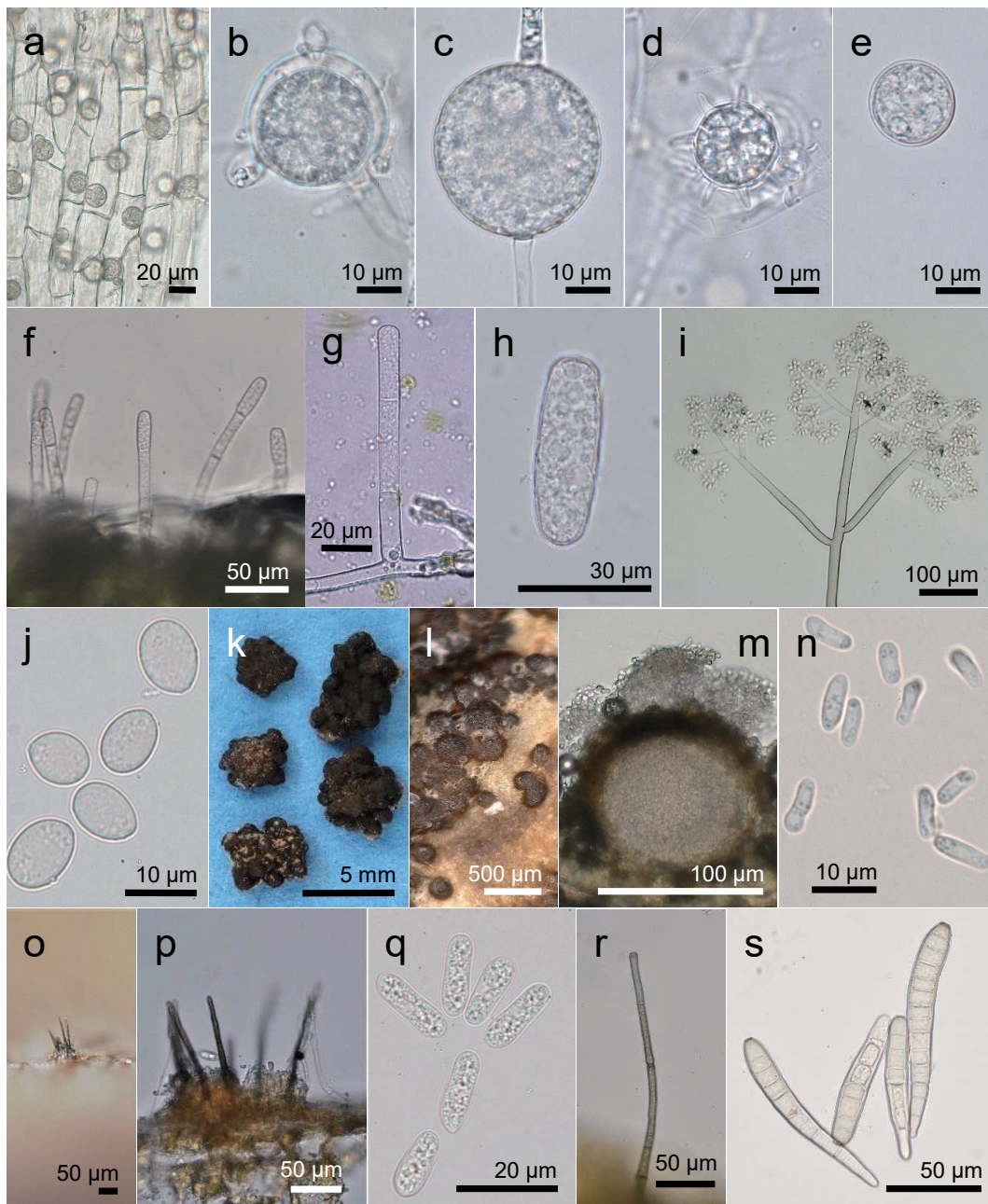


Fig. 2. Morphology of pathogens

a. Hyphal swellings of *Globisporangium* sp. in infected root cells, **b.** Oogonium and antheridia of *Pythium myriotylum*, **c.** Hyphal swelling of *Globisporangium splendens*, **d.** Oogonium of *Globisporangium spinosum*, **e.** Hyphal swelling of *Globisporangium* sp., **f.** Conidiophore of *Oidium* sp., **g.** Conidiophore of *Oidium* sp., **h.** Conidium of *Oidium* sp., **i.** Conidiophore of *Botrytis cinerea*, **j.** Conidia of *Botrytis cinerea*, **k.** Sclerotia of *Botrytis cinerea*, **l.** Pycnidia of *Phoma* sp., **m.** Pycnidia and conidia of *Phoma* sp., **n.** Conidia of *Phoma* sp., **o.** Blackish brown acervuli with setae of *Glomerella cingulata*, **p.** Acervuli of *Glomerella cingulata*, **q.** Conidia of *Glomerella cingulata*, **r.** Conidiophore of *Corynespora cassiicola*, **s.** Conidia of *Corynespora cassiicola*.

Gray mold (pathogen: *Botrytis cinerea*)

Under high humidity conditions, sporulation of *B. cinerea* is formed on lesions.

1. Symptoms

Gray mold occurs on leaves (Fig. 1 k, l), inflorescences (Fig. 1 m), and flower buds (Fig. 1 n).

2. Distribution

The pathogen is distributed worldwide (Table 1). It has been recorded on hydrangea in Niigata (Arai 1996), Hokkaido (Narita 1998) and Shimane Prefectures (Nagashima et al. 2021b) in Japan.

3. Occurrence

Botrytis cinerea has a wide host range. Conidia (Fig. 2 j) are formed on the conidiophores (Fig. 2 i) and spread by air flow to infect the plants. This disease occurs easily on wounded tissue or through colonization with dead plant tissues. Environmental factors such as long durations of leaf wetness and high relative humidity promote infection and disease development (Dik & Wubben 2004).

4. Control

Keeping a low relative humidity by ventilation, heat, and/or increasing plant spacing is very important for disease control. Additionally, to shorten the duration of leaf wetness, watering in the morning is recommended. Removing diseased tissues from plants reduces an infection source. Fungicide spray before infection or disease development is effective, but *B. cinerea* is known to develop resistance to fungicides. Growers need to use mixtures and rotations among FRAC groups (a group of fungicides with the same mode of action).

Leaf spot/stem rot (pathogens: *Phoma exigua*, *Phoma* spp.)

1. Symptoms

The disease occurs on leaves and stems. Leaves initially show small necrotic spots, and the lesions develop into large, circular to irregular, grayish-brown zonate patterns (Fig. 1 o, p). The size and color of the lesions vary depending on the cultivar (Li et al. 2016). Stems show brown lesions, followed by wilt and death (Fig. 1 q). Many pycnidia, brown to blackish brown, are formed on the lesion (Fig. 2 l, m).

2. Distribution

The pathogens are only recorded on hydrangea in Japan, Italy and USA (Table 1). But *Phoma exigua*, on the other plants, is distributed worldwide (Boerema et al. 2004). In Japan, *Phoma exigua* is recorded on hydrangea in Toyama (Takano 1994), Gunma (Ikeda et al. 2010), and Ibaraki Prefectures (NARO Genebank 2022b), and *Phoma* sp. is recorded in Gunma (Ikeda et al. 2010), Kanagawa (NARO Genebank 2022b), and Shimane Prefectures (Fig. 1 o, p, q; Fig. 2 l, m, n).

3. Occurrence

Phoma exigua overwinters as pycnidia and hyphae in diseased leaves (Kishi 1998). Pycnidia were formed on stem rot of hydrangea caused by *Phoma exigua* and *Phoma* spp. (Ikeda et al. 2010), so these pathogens may also overwinter in diseased stems. Conidia (Fig. 2 n) formed in pycnidia are spread by splashed water.

4. Control

Pruning of high-density stems improves air flow around the basal stems. Removing diseased leaves and stems reduces infection sources.

Anthracnose (pathogen: *Colletotrichum destructivum*, *Glomerella cingulata*)

1. Symptoms

Anthracnose occurs on leaves and petals (sepals). The disease causes many leaf spots that are small (1 mm-3 mm in diameter), circular, somewhat sunken, and grayish white in the center of the lesion, and purple-brown at the edge of the lesion (Fig. 1 r, s). The lesions fuse with each other to form large irregular spots, which may have a zonate pattern. The petals have many spots that are small, light brown to brown, and surrounded by a purple-brown edge. Some blackish brown acervuli (Fig. 2 o, p), that sometimes have setae, are formed on the center of the lesion.

2. Distribution

Colletotrichum destructivum has been only recorded in Japan, including Miyagi, Tokyo, Ibaraki, Gunma, and Chiba Prefectures (Table 1, NARO Genebank 2022b). *Glomerella cingulata* distributes worldwide (Table 1), and has been recorded on hydrangea in Tokyo, Chiba (Nakamura 1970), Fukuoka, Gunma (NARO Genebank 2022b) and Shimane Prefectures (Fig. 1 r, s; Fig. 2 o, p, q) in Japan.

3. Occurrence

Glomerella cingulata has a very broad host range. The pathogen overwinters in diseased leaves and stems of hydrangea and host plants (Kishi 1998, Li et al. 2016). The conidia (Fig. 2 q) formed in acervuli on the lesions are spread by water splashed on the leaves and petals.

4. Control

Removing diseased leaves and petals reduces the infection sources. Fungicide spray before the infection is effective.

Leaf spot (pathogen: *Corynespora cassiicola*)

1. Symptoms

Corynespora cassiicola mainly occurs on leaves, sometimes on petals (sepals). Leaves initially show small reddish-purple to brown spots. The spots gradually enlarge into a brown, zonate pattern, and the center of the lesions turn white (Fig. 1 t, u). Leaves with many spots defoliate early. Conidiophores (Fig. 2 r) and conidia (Fig. 2 s) are formed on the lesions.

2. Distribution

The pathogen is distributed worldwide (Table 1). It has been recorded in Japan, including in Okayama (Kasuyama & Idei 1987), Kanagawa, Gunma, Tottori, Chiba, Miyazaki (NARO Genebank 2022b), and Shimane Prefectures (Fig. 1 t, u; Fig. 2 r, s) in Japan.

3. Occurrence

The pathogen overwinters in infected leaves, stems and buds (Kishi 1998, Li et al. 2016). Conidia are disseminated by air currents and infect the plants.

4. Control

Using disease-free cuttings is very important to prevent the disease. Pruning of stems and adequate spacing improve air movement around plants. Irrigation should be done at the base of the plant so as not to wet the leaves. Growers should remove the diseased leaves as soon as possible.

Discussion

The present review demonstrated that there are at least 71 hydrangea diseases in Japan (Table 1). The causal agents of the diseases are 2 viruses, 2 phytoplasmas, 3 bacteria, 5 oomycetes, and 59 fungi. Among the 71 of them, 39 have only been recorded in Japan. Approximately 20 of these causal agents can also be found in Shimane Prefecture (Nagashima unpublished). At least 17 viruses, 2 phytoplasmas, 8 bacteria, 14 oomycetes, and 167 fungi were found on hydrangeas throughout the world (Baysal-Gurel et al. 2016, Chen et al. 2022, Cottyn et al. 2021, Gardan & Dorkar 1985, Hilton 2000, Machado Caballero et al. 2009, Menzel et al. 2016, NARO Genebank 2022a, Parrella & Troiano 2022, Uddin et al. 1996, USDA ARS 2022, Veerakone et al. 2012). Therefore, Japan has approximately one-third of the world's recorded hydrangea diseases, including the local causal agents. The large number of known hydrangea diseases in Japan is primarily attributable to their long history of disease studies, beginning in 1892 (Table 1,

Tsukiboshi et al. 2007). One of the oldest records of hydrangea diseases is *Pucciniastrum hydrangeae* on *H. paniculata* in 1892 (Tsukiboshi et al. 2007). The high humidity and temperature ranges of Japan are also involved in pathogen diversity on hydrangea as well as on other plants (NARO Genebank 2022a).

Development of new cultivars is one of the factors of hydrangea disease occurrences in recent years in Japan. Applications for hydrangea cultivar registration in the country have increased from 60 in 1991-2000 to 183 in 2001-2010, and 321 in 2011-2020 (MAFF 2022a). Some of them are of high value and increase farmers' profit (Ishii 2019). However, new cultivars are often susceptible to several diseases that have not occurred earlier (Nagashima et al. 2021a). For example, the hydrangea cultivar "Mangekyo" was affected by stem and root rot only 2 years after it began commercial cultivation (Nagashima et al. 2021a).

Increased pot cultivation is also having an influence on hydrangea diseases in Japan. Most of the hydrangea diseases recently recorded in the country occurred on potted plants grown in greenhouses. The major pathogens on potted *H. macrophylla* are oomycetes, including *Pythium myriotylum*, *Globisporangium splendens*, *G. spinosum*, *Globisporangium* sp. (Nagashima et al. 2021a), and *Phytophthora hedraiondra* (Yosilia et al. 2020). These oomycete pathogens prefer high humidity and high-density cultivation. This review also revealed that bacterial leaf spot caused by *Acidovorax valerianellae* is common on hydrangeas in Japan (Ikeda et al. 2009, Takikawa et al. 2008). *A. valerianellae* is a major bacterial pathogen and can survive in flower buds during winter (Ikeda & Furuya 2020). The greenhouse pot of hydrangea is often cultivated under humid, high-temperature conditions with intensive, high-density management. Such growing environments may have enhanced the development of these oomycete and bacterial pathogens of hydrangea in recent years in Japan.

Japan has many hydrangea gardens in temples, shrines, parks, etc. (Kawarada et al. 2010). In Shimane Prefecture, anthracnose, leaf spot caused by *Corynespora cassiicola*, powdery mildew, and gray mold are common diseases of hydrangea in gardens. Most of the diseases occur during the rainy season, and they may occur every year (Kishi 1998). Because these diseases damage not only leaves but also flowers, their ornamental value may be considerably reduced (Kishi 1998). For disease control, it is important to prune stems to improve ventilation.

Chemical control is necessary for potted hydrangeas to keep their quality at an adequate level. Some chemicals against stem and root rot or bacterial leaf spot disease have been recently registered (Ikeda et al. 2022,

Nagashima et al. 2020). Because limited chemicals against hydrangea diseases are registered in Japan (MAFF 2022b), chemical control remains restricted for a few diseases. Effective chemicals against hydrangea diseases should be further studied for their practical use, especially for major hydrangea diseases such as powdery mildew, bacterial leaf spot, leaf spot caused by *Corynespora cassiicola*, and leaf spot/stem rot caused by *Phoma* spp.

Conclusions

This review has revealed the diversity and uniqueness of hydrangea diseases in Japan. Several high-value cultivars have recently been developed in common hydrangea that are susceptible to diseases. Culturing hydrangeas in pots can also enhance the development of several diseases. Thus, concentrating on disease control in new cultivars grown in greenhouse pot cultivation may result in increased hydrangea production in Japan.

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