

BOTRYTIS GENUS FUNGI AS CAUSAL AGENTS OF LEGUME DISEASES: A REVIEW

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Abstract

Grain legumes are important crops for the diversification of European farming system. In Latvia, the areas of faba beans (*Vicia faba*) and field peas (*Pisum sativum*) are increasing and legumes that have not been previously cultivated are sown. Globally, the important causal agent of legume diseases belongs to the genus *Botrytis*. *Botrytis* spp. cause significant losses in faba beans and infect a wide range of legume crops. Currently, the composition, pathogenicity and biological characteristics of *Botrytis* species in legumes in Latvia are not known. The aim of this study was to summarize the information about *Botrytis* spp. on legumes, using monographic method. The researches carried out all over the world show a high genetical diversity of *Botrytis cinerea*. Non-host specific *B. cinerea* has been found on 586 plant genera, including many legume crops. *B. cinerea* causes gray mold on leaves and pods of field peas, gray mold on pods of faba beans, and chocolate spot of faba bean leaves. *B. fabiae* can infect plants from *Fabaceae* family. *B. fabiopsis* is known as a pathogen of faba beans. *B. fabiopsis* has been observed in Latvia, but no information is available on its presence in Europe. *B. pseudocinerea* has been found on beans, peas, and clover (*Trifolium*). Some other *Botrytis* spp. have been detected on legumes; however, their occurrence and importance are not clear. Summary of existing knowledge about *Botrytis* spp. on legumes is necessary to continue investigations about the diversity and economic importance of *Botrytis* spp. in legumes.

Key words: cool season legumes, faba beans, chocolate spot, gray mold.

Introduction

Legumes is an important crop all over Europe, and sowing areas have been increasing during the last years. Leaf and pod diseases is one of the most important yield-limiting factors. Diseases caused by *Didymella* spp., *Fusarium* spp., *Sclerotinia sclerotiorum*, *Alternaria* spp., and *Stemphylium* spp. are widespread and harmful all over the world. The occurrence of pathogens depends on hosts and meteorological conditions, but fungi from the genus *Botrytis* infect all species of *Fabaecae*. *Botrytis* is one of the most studied necrotrophic fungi; nevertheless, it can cause considerable economic losses – pathogenicity and biological properties of different *Botrytis* species are still unclear. A high genetical and morphological diversity has been observed within this genus; therefore, knowledge of *Botrytis* species and their life cycles is important. The aim of this study was to summarize the information about *Botrytis* species, their harmfulness and legume hosts, to determine the necessity for future research in Latvia.

Materials and Methods

In the present study, the monographic method was used. The literature on the biology and taxonomy of *Botrytis* spp. and the diseases they cause was analysed. The results of research on *Botrytis* species in legumes carried out in different parts of the world were summarized.

Results and Discussion

Importance of legumes in Europe and Latvia

Cropping systems in Europe are heavily dominated by cereals and oilseed rape (*Brassica napus*). These

two crop groups have the highest profit margins and therefore are favoured by European farmers. Unfortunately, this is one of the main reasons why European cropping systems lack crop diversity. Legume grain crops provide various benefits for cropping systems from which the most notable is the reduced need for synthetic fertilisers (Watson *et al.*, 2017).

Grain legumes are slowly regaining their position in the European agriculture. Most of the legumes that are bred in Europe are field peas (*Pisum sativum*), faba beans (*Vicia faba*), sweet lupines (*Lupinus albus*), chickpeas (*Cicer arietinum*), lentils (*Lens culinaris*), and vetches (*Vicia sativa*) (Eurostat, 2018). With political support of the European Union, the total sown area of grain legumes in Europe is increasing. In the last 10 years, the area of peas has almost doubled – from 1.5 million ha in 2007 to 2.7 million ha in 2017. A more rapid expansion is seen in the niche of grain legumes such as lentil and chickpea. The area of chickpea fields has seen rapid expansion: in 2007, chickpea area was only 67.6 thousand ha, whereas in 2017, it covered 562.6 thousand ha. The development of the area of lentil is not quite as rapid as that of chickpea; however, the growth is still considerable – from 37.3 thousand ha in 2007 to 241.9 thousand ha in 2017. Soybean (*Glycine max*) is one of the most important and widespread grain legumes worldwide, e.g., in Europe, from 2007 to 2017, soybean area tripled – from 1.9 million ha to 5.7 million ha. Lupine is the only grain legume in Europe whose sown areas start to decrease – after reaching its peak in 2015, when the lupine area was 370 thousand ha, it fell down to 274.4 thousand ha in

2017. In countries where soybean or pea growing is not suitable or causes inconveniences in the planning of harvesting, faba bean takes an important place in grain legume proportion (FAO, 2017). Faba bean is a valuable legume crop, which can be grown as a grain crop or a green-manure legume in numerous cropping systems across the globe. The seeds are used for human consumption or animal feed and are highly nutritious because of the high protein content (up to 35%) and the great diversity of nutrient and bioactive compound content (Karkanis *et al.*, 2018). Faba bean is a typical cereal pre-crop in the European cropping systems and is usually followed by one or two cereals (Karkanis *et al.*, 2018). Despite the positive characteristics of faba bean, its global sown area declined from 3.7 million ha in 1980 to 2.4 million ha in 2006, and from then, there have been no considerable changes in the global sown area of faba bean (FAO, 2019). In contrast, the total area of faba beans in Latvia, due to changes in the agricultural policy of the European Union, has started to grow rapidly – from 4.4 thousand ha in 2013 to 42.5 thousand ha in 2017 (Central Statistical Bureau of Latvia, 2018).

In Latvia, sowings of faba beans and field peas are increasing, and lupines and vetches are grown in small areas (Central Statistical Bureau of Latvia, 2018). Lucerne (*Medicago sativa*), lupine, red clover (*Trifolium pratense*), white clover (*Trifolium repens*), alsike clover (*Trifolium hybridum*), fodder galega (*Galega orientalis*) (also common as eastern galega), and honey clover (*Melilotus albus*) are grown as fodder legumes and herbaceous forage under the agronomical and ecological conditions of Latvia (Karklins & Lipenite, 2015).

Diseases is one of the most important factors that limit legume production. There are several leaf and pod diseases caused by different pathogens (*Didymella* spp., *Fusarium* spp., *Sclerotinia sclerotiorum*, *Alternaria* spp., and *Stemphylium* spp.), but the most important diseases are caused by fungi from the genus *Botrytis*, which infects all species of legumes. Diseases, which are caused by these pathogens are the most widespread also in Latvia (Pluduma-Paunina *et al.*, 2018).

Taxonomy and phylogeny of Botrytis genus

Botrytis spp. are worldwide-distributed plant pathogens with a high genetic diversity. *Botrytis* genus is classified in the kingdom *Fungi*, phylum *Ascomycota*, subphylum *Pezizomycotina*, class *Leotiomycetes*, order *Helotiales*, family *Sclerotiniaceae*. There is also sexual stage – *Botryotinia* spp., asexual name *Botrytis* should be used according to the rules of the International Code of Nomenclature (Rossman, 2014). The genus *Botrytis* includes about 30 species, one hybrid species *B. allii* (*B. byssoides* × *B. aclada*), and species complexes (Yohalem, Nielsen, & Nicolaisen, 2003; Walker, 2016); investigations in

taxonomy are still continuing.

The majority of *Botrytis* species were described at the end of the 19th and in the 20th centuries on the basis of fungal morphology. *Botrytis* spp. have high morphological diversity – colonies in pure culture vary in colour and morphology. Species are difficult to distinguish morphologically; therefore, molecular identification methods succeed in discovering new species and compiling phylogenetic trees. New species are discovered and described occasionally worldwide in different crops and wild plants (Zhang *et al.*, 2010a; Li *et al.*, 2012). At least seven species have been found or differentiated in the last decade (Walker, 2016).

Botrytis spp. were grouped into two distinct phylogenetic groups (clades) by M. Staats *et al.* (2005) using combined phylogenetic analysis of three protein-coding genes. Clade 1 includes species that infect dicots, but species from Clade 2 infect either dicots or monocots. Since the establishment of the clades, several new species have been described. At this moment, Clade 1 includes non-host-specific *B. cinerea* and *B. pseudocinerea* and host-specific species *B. fabae*, *B. calthae*, *B. sinoviticola* and *B. californica*. *Botrytis* species from different subclades, for example *B. fabae* and *B. fabiopsis*, can infect one hostplant (Zhang *et al.*, 2016). Researches are still in progress to find genes for the identification of species from both clades (Hyde *et al.*, 2014).

Botrytis species are usually named depending on the host plant name. However, it has been found that host and pathogen phylogenies are not congruent (Staats, van Baarlen, & van Kan, 2005). It proves that both organisms do not co-evaluate to match resistance genes in host with virulence genes in the pathogen. Host shifts explain the low congruence between *Botrytis* species and their hosts (Staats, van Baarlen, & van Kan, 2005).

Characterization of Botrytis genus as a plant pathogen

Fungi of the genus *Botrytis* might have asexual (anamorph) and sexual (teleomorph) development stages of the life cycle. In asexual stage, fungi produce macroconidia and microconidia. The majority of *Botrytis* species produce sclerotia, which are able to overwinter and survive in extreme conditions. Usually, sclerotia germinate, produce mycelium and conidia, and continue asexual stage. To induce the sexual reproductive cycle and produce apothecia, microconidia should fertilize sclerotia (Faretra & Antonacci, 1987; Fukumori, Nakajima, & Akutsu, 2004). Not all *Botrytis* species produce ascospores. It has been observed that the sexual stage disappears because of negative selection (Willetts, 1997). The ascospores need moisture and have low UV-tolerance (Willetts, 1997). This confirms the necessity for additional research of *Botrytis* spp. in different regions

of the globe with various meteorological conditions.

All *Botrytis* species are necrotrophs and kill plant cells to metabolize them. Most studied is the pathogenesis of *B. cinerea*, but the infection process is similar to other *Botrytis* spp. The pathogen is able to penetrate through the plant cuticle or stromata openings. Fungi are opportunists and often infect damaged tissues or sites infected by other pathogens (Kars & van Kan, 2007). *Botrytis* spp. produce enzymes (oxidases, cutinases, and lipases) to penetrate into plant (Tenberge, 2007). Epidermal cells are destroyed by metabolites such as laccases, proteases, and pectinases. The pathogen causes programmed host–plant cell death to attack and take the nutrients.

There are known several *Botrytis* spp. that have two forms of the disease – aggressive and non-aggressive (Price, 1970; Hargreaves, Mansfield, & Rossall, 1977; Harrison, 1981). Optimal weather conditions can cause phase transformation, resulting in large-scale damage to plants in the form of small restricted spots. During prolonged periods of high humidity and moisture, on the leaves of faba beans, aggressive forms of chocolate spot disease have been observed (Park & Lopetinsk, 1999; Kaur *et al.*, 2018).

Botrytis species are necrotrophic facultative pathogens; however, recent studies have shown the ability of some species to live in plant tissue as endophytes. Six undescribed haplotypes of *Botrytis* have been found during the studies (Shipunov *et al.*, 2008). Many other undescribed species could be concealed in plant tissues as endophytes without causing any symptoms of infection.

Botrytis spp. in legumes

Botrytis fungi have been observed worldwide everywhere the host plants grow (Jarvis, 1977). As Y. Elad *et al.* (2016) summarized, *Botrytis* spp. have been recorded on 596 genera of vascular plants. In the same study, the authors suggest that *Botrytis* occurrence is related to the softness and tenderness of plant tissues. Leaves of legumes mainly are thick and brittle, and any injuries as mechanical or by insects can induce *Botrytis* infection (Williamson *et al.*, 2007). Drought stress makes legumes weak and easily attacked by pathogens, which does not cause damages in normal growing conditions (Ahmed *et al.*, 2011).

At present, only two species are known that are not strictly specialized plant pathogens – *B. cinerea* (can infect more than 235 plant species of eudicotyledons) and *B. pseudocinerea*, that have multiple plant hosts (Williamson *et al.*, 2007; Walker *et al.*, 2011; Elad *et al.*, 2016). *B. cinerea* has been found on 586 plant genera (Elad *et al.*, 2016). *B. fabae* is able to infect plants from several plant genera, but all of them are related to *Fabaceae* family. Other *Botrytis* species are specialized pathogens that are able to infect one plant species or a few species from one genus.

B. cinerea

The information on the occurrence of *B. cinerea* Pers. in *Fabaceae* plant family was collected by Y. Elad *et al.* (2016). *B. cinerea* causes gray mold on lentils (Davidson *et al.*, 2004; Tivoli *et al.*, 2006), chickpeas (Pande *et al.*, 2001; Davidson *et al.*, 2007), vetches, beans, peas, clover (Grigaliūnaitė, 2001), galega, soybean, and severe species of *Lupinus* genus: *L. albus*, *L. angustifolius*, *L. hirsutus*, *L. luteus*, *L. mutabilis*, *L. polyphyllus*, *L. × regalis*. *B. cinerea* leaf blight and gray mold have been found on eastern clover (*Trifolium dasyurum*) (Loi *et al.*, 2007), white clover and subterranean clover (*Trifolium subterraneum*) (Elad *et al.*, 2016), honey clover, and has been isolated from lesions on roots (Cormack, 1946). *B. cinerea* causes blossom blight in lucerne (Huang, Kokko, & Erickson, 1999; Li *et al.*, 2004).

B. cinerea causes grey mold on field pea pods (Dobson & Heath, 1991) and has been isolated from pea flowers (Ma & Michailides, 2005). Gray mold of peas, mostly on leaves, has been commonly noted during wet seasons in Canada (Basu *et al.*, 1973). *B. cinerea* infects flowers and pods of bean (Deverall & Wood, 1961; Davidson *et al.*, 2007) and leaves (Zhang *et al.*, 2010). Different isolates of *B. cinerea* may significantly differ in pathogenicity on various host plants (Mirzaei *et al.*, 2009). Diseases caused by *B. cinerea* are difficult to control, because they have many host plants that act as a source of infection.

Symptoms of gray mold caused by *B. cinerea* are similar on different hosts. The infection develops on leaves, plant stem, crown, flowers and pods, and, as a result, the amount and quality of yield reduce or the whole plant can dry out (Bayaa & Erskine, 1998; Taylor *et al.*, 2007). *Botrytis* spp. has been isolated from discolored and shrivelled seeds (Kaiser, 1992). Disease symptoms are brown or blanched water-soaking lesions on leaves and fruits. Grey masses of conidia cover lesions on plants and pods (Bayaa & Erskine, 1998). Conidia land on flowers, germinate, and the infection penetrates into the closely related plant tissues (Biddle & Cattlin, 2007); therefore, pods are often infected. Cool and moist weather conditions are favorable for the spreading of infection through the plant. More harmful are early infections – as a result of infection and enzymatic degradation, considerable number of lesions may occur on plants (Emden, Ball, & Rao, 1988).

B. fabae

B. fabae is one of the most studied pathogen of faba beans; however, it is able to infect plants from *Fabaceae* plant family and has been also found on the genera of *Vicia*, *Pisum*, *Lens*, *Phaseolus*, and *Trifolium* (Jarvis, 1977; You *et al.*, 2009; Elad *et al.*, 2016). *B. fabae* has been recorded on common vetch. Chocolate spot caused by *B. fabae* has been observed on field peas and eastern clover (Elad *et al.*, 2016).

Chocolate spot caused by *Botrytis* spp. is the most common and important disease of faba beans. *B. fabae* is able to infect all overground plant parts, and, likewise, *B. cinerea* is worldwide distributed. *B. fabae* is more aggressive for faba beans because of its ability to attack, penetrate and metabolize plant tissues as a specialized pathogen (Jellis & Bond, 1980; Davidson *et al.*, 2007). Symptoms are numerous red-to-dark brown spots, generally on leaves and pods. The infection causes leaf damage, seed and pod reduction, or total crop failure at severe epidemics. In cool and humid conditions, small spots merge into larger lesions (Harrison, 1981). Prolonged wet conditions, when relative humidity is 92 – 100%, are more favorable for chocolate spot development (Harrison *et al.*, 1984; Davidson *et al.*, 2007). Faba bean infection at the growth stages of flowering and early pod development causes a significant reduction in seed yield from the plant and pod number decrement (Griffiths & Amin, 1977). Recorded yield losses in different parts of the world have reached 50 – 90%. The yield losses may even reach 100% if the yield formation is disturbed (Davidson *et al.*, 2007).

Optimal temperature of *B. fabae* growth, sporulation, and development is 22 °C (Terefe *et al.*, 2015).

B. fabiopsis

For the first time, *B. fabiopsis* was described in China by J. Zhang *et al.* (2010). Symptoms caused by unknown species on faba bean leaves were similar to *B. fabae* lesions but smaller than *B. cinerea* lesions. Morphological characteristics differed between the species. Mycelial growth temperature ranged between 5 °C and 10 °C, and the optimal temperature was 20 °C. The authors report that *B. fabiopsis* infected faba beans and was not found on other crops near the bean field, unlike *B. cinerea* that could infect some winter crops like peas, wheat (*Triticum*), and oilseed rape. *B. fabiopsis* is incompletely studied, and there is no information available on the presence of *B. fabiopsis* in Europe. The occurrence of *B. fabiopsis* in other legumes is unknown, and no researches have been made after detecting the new species in China. The identification of the causal agent of chocolate spot under field conditions is impossible; therefore, DNA-based analyses are necessary for species identification. Recent studies of chocolate spot of faba beans show that *B. fabiopsis* has been found in Latvia (Bankina *et al.*, 2017).

B. pseudocinerea

Earlier *B. pseudocinerea* has been classified as part of *B. cinerea* species complex or Group I of *B. cinerea sensu lato* (Leroux *et al.*, 2002; Beever & Weeds, 2007). Fournier *et al.* (2003) found genetic differentiation between both groups. The first time the species was described by Walker *et al.* (2011), who found the fungus in French vineyards in complex with

B. cinerea. This complex can be observed in faba beans and also on peas and in clover. Five strains of *B. pseudocinerea* were found in a faba bean field in Germany (Plesken *et al.*, 2015). *B. pseudocinerea* and *B. cinerea* differ in resistance pattern to fungicides (Fournier *et al.*, 2003).

B. pseudocinerea is different from *B. cinerea* genetically, but similar in morphology. No significant morphological differences were found between *B. cinerea* and *B. pseudocinerea* (Fekete *et al.*, 2012).

B. pseudocinerea showed unique overlapping between isolates in vegetative compatibility tests, possibly due to the low genetic diversity (Fekete *et al.*, 2012). Also, gene transfers between *B. cinerea* and *B. pseudocinerea* strains can be possible, as E. Fekete *et al.* (2012) suggested.

Other species

B. caroliniana was detected on blackberries in 2010 (Li *et al.*, 2012). Pathogenicity tests showed the ability of *B. caroliniana* to infect faba bean leaves. Also A. S. Walker (2016) suggested, based on unpublished data, that probably *B. caroliniana* can be pathogenic to faba beans. *B. caroliniana* is genetically closely related to *B. fabiopsis* and they can infect faba beans (Li *et al.*, 2012).

B. anthophila was discovered in red clover in 1913. The fungus develops on plant flowers and petals and infects seeds. *B. anthophila* was found on red clover flowers and seeds in Lithuania (Grigaliūnaitė, 2001).

B. pyriformis could infect faba bean leaves *in vitro* during pathogenicity tests using agar plugs with mycelium and conidia suspension (Zhang *et al.*, 2016). There is no information about the occurrence of the fungus on broad beans in nature.

Pathogenicity tests showed the ability of *B. aclada*, *B. euroamericana*, and *B. paeoniae* to form lesions on faba bean leaves (Garfinkel *et al.*, 2017). *B. aclada* is a specialized pathogen of onion (*Allium cepa*) but also could cause primary lesions on the non-host plant that were significantly smaller than *B. cinerea*, *B. euroamericana*, and *B. paeoniae* caused lesions. The role of *B. euroamericana* in broad beans is unclear, and no further researches have been made to determine its pathogenicity in field conditions.

Conclusions

1. Pathogens from genus *Botrytis* are common causal agents of diseases of different legumes cultivated in Latvia, Europe, and worldwide. Studies show that one legume crop can be infected with several *Botrytis* species, which differ in their pathogenicity and aggressiveness.
2. *B. cinerea*, *B. fabae*, and *B. fabiopsis* are faba bean pathogens, but their significance should be clarified. *B. pseudocinerea* has been found on faba beans in field conditions, and it might

- be a potential pathogen of different legumes. *B. caroliniana* and *B. euroamericana* infected faba beans during pathogenicity tests *in vitro*. *B. aclada* and *B. paeoniae* formed primary lesions on faba bean leaves, but their role in infection of legumes is uncertain.
3. Basic knowledge about diversity of *Botrytis* spp., their distribution and biological properties is required to understand the life cycles of the species and to establish an economically and biologically based control of the causes of this species diseases.
 4. Further investigations are required to determine *Botrytis* species on legumes in Latvia, investigate the occurrence and pathogenicity of the fungi and select plant protection methods to control *Botrytis* infection in legumes.

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