ALTERNARIA BLACK SPOT OF CRUCIFERS: 
SYMPTOMS, IMPORTANCE OF DISEASE, 
AND PERSPECTIVES OF RESISTANCE BREEDING

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Summary
Alternaria black spot of cruciferous vegetables, incited by different species of Alternaria, remains an increasing threat to Brassicaceae crops throughout the world, including Poland. Brassica plants are attacked by conidia of A. brassicae (Berk.) Sacc., A. brassicicola (Schw.) Wiltsh., A. raphani Groves & Skolko, and A. alternata (Fr.) Kreissler. The pathogens have a wide spectrum of hosts, such as head cabbage, Chinese cabbage, cauliflower, broccoli, and other crucifers including cultivated and wild grown plants. Alternaria pathogens usually cause damping-off of seedlings, spotting of leaves of cabbages, blackleg of heads of cabbages, and spotting of cauliflower curds and broccoli florets. In oilseed rape, A. brassicae is the dominant invasive species, while in the cruciferous vegetables, both species, A. brassicae, and A. brassicicola are encountered. Infected seeds with spores on the seed coat or mycelium under the seed coat are the main means of distribution for these pathogens. The fungus can overwinter on susceptible weeds or crop debris and on seed plants, as well as on stocklings.

Methods for disease prevention and control are based on combining agricultural management practices with chemical control. Using disease-free seeds or seeds treated with fungicides can greatly reduce disease incidence. After appearance of the first symptoms of disease, stringent fungicide spray program is an effective way to reduce losses. Many authors seem to agree, that the most economically feasible method of disease control is the development of resistant Brassicaceae crops varieties, as transgenic approach proved unsuccessful. Due to our increasing understanding of pathogen-host plant interactions, identification of resistance sources, and assessment of the resistance trait inheritance mode, breeding programs of Brassica crops for Alternaria resistance can be enhanced. This is of particular importance since recent years experience dynamic development of ecological and integrated plant production with an emphasis on plant biotic stress resistance. Highly resistant genetic resources have not been reported in Brassica cultivated species, although some varieties differ in their resistance/susceptibility level.

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Strong cross-incompatibility, polygenic background of the resistance (additive and dominant gene interactions), as well as the differences in ploidy between the *Brassica* species of interest, render the transfer of *Alternaria* resistance from the wild species into the cultivated forms difficult. Additionally, it is often connected with employment of *in vitro* hybridization techniques, including somatic hybridization, embryo and ovary rescue, or protoplast fusion.

**INTRODUCTION**

Cruciferous plants (*Brassicaceae*) worldwide are severely affected by the *Alternaria* fungi. *A. brassicicola* (Berk.) Sacc., *A. brassicae* (Schw.) Wilth., *A. raphani* Groves and Skolko, and *A. alternata* (Fr.) Kreissler belong to species of major negative influence on *Brassicaceae* plants. Although both, *A. brassicicola* and *A. brassicae* occur on oleiferous and vegetable (oleraceous) *Brassicas*, the former is the dominant invasive species of the vegetable *Brassicas*, while the oleiferous crucifers are primary hosts for the latter fungus (Maude & Humpherson-Jones 1980, Humpherson-Jones 1989).

Both most common *Alternaria* pathogens usually cause black spot disease, manifested by damping-off of seedlings, spotting of leaves of cabbages, blackleg of heads of cabbages (head cabbage and Chinese), and spotting/browning of cauliflower curds and broccoli florets. Black spot is the most common disease in the crucifers plantations located in tropical and sub-tropical regions. Due to weather conditions conducive to infection (see below), however, the disease constitutes a serious problem in crucifers plant production in long-lasting high humidity or intensive rains regions, including Poland.

*A. brassicicola* and *A. brassicae* cause severe economic losses in several different ways (Humpherson-Jones & Maude 1982, Humpherson-Jones 1989). Seed infection causes reduced germination and seedling vigour, in addition to pre- and post-emergence damping-off, and affects the sale and use of infected/infested seed. Lesions on leaves, stems, and siliques reduce the photosynthetic area and accelerate senescence in the plant. These pathogens are responsible for major seed yield losses in the oleraceous *Brassicas* and this is the most important component of their economic impact. The unsightly cosmetic blemishing or rotting of the head or wrapper leaves in vegetable *Brassicas* as a consequence of pathogens’ toxins and disease causes downgrading and crop losses in both fresh and stored produce. *A. brassicicola* often occurs in conjunction with *A. brassicae* and some other pathogens of the *Brassicaceae*. This confounds precise estimates of losses caused individually by this pathogen in the field.

In Europe, alone the seed losses due to both pathogens were estimated at up to 86% in *B. oleracea* in several years (Maude & Humpherson-Jones 1980, Humpherson-Jones 1989). Under Polish climate conditions, the disease takes particularly high toll on
the late and medium-late varieties of head-cabbage grown for sauerkraut processing, as well as for storage. Cabbage heads with characteristic symptoms of Alternaria black spot do not store well, and their processing value is very low. This translates onto significant economic impact of the disease: In 2010, Polish cabbages and other Brassicas production ranked 7th, while cauliflower and broccoli ranked 8th globally (1141200 tonnes and 252325 tonnes, respectively) with net worth of production of Int.$171 M and Int.$60,5 M, respectively (FAOSTAT: http://faostat.fao.org).

Alternaria prevention and control methods include combining the proper agro-technique with chemical protection. An essential disease prevention method is production of healthy seeds, obtained from plantations with heavy fungicide protection. In the 2-year lasting crucifers seed production periods, good effects of protection against Alternaria infections during the 1st year of growth were expedited by fungicides containing iprodione as an active ingredient (Maude et al. 1984, Survilienė et al. 2010). In Poland, the only product containing it is Seed Protector T 75DS WS (Zaprawa Nasienna). Since both pathogens survive on crop debris, seeds, and in association with weed hosts (Humpherson-Jones & Maude 1982, Humpherson-Jones 1989), crop debris management (for example through crop rotation and deep tillage) and use of clean seed and proper weed control should alleviate the disease. After appearance of disease symptoms, one may achieve limitation of the infection by repeated spray with fungicides containing strobilurines as active ingredients (Amistar 250 SC, Signum 33 WG, Zato 50 WG) and fungicides based on iprodione (Rovral FLO 255 SC) (Maude et al. 1984, Survilienė et al. 2010). This method, however, carries an economic disadvantage and may prove ineffective under pathogen infection-conducive weather conditions, particularly among the seed crops. An alternative protection method to be employed is use of antagonistic fungi; deployment of Aureobasidium pullulans and Epicoccum nigrum on the crucifers leaves reduced the infection level under controlled conditions (Pace & Campbell 1974). Field studies concerning the biological control efficacy are yet to be carried out.

Pathogen profile and infection progress

The current classification of Alternaria fungi is as follows: Kingdom Fungi, Phylum Ascomycota; Subdivision Pezizomycotina; Class Dothideomycetes; Order Pleosporales; Family Pleosporaceae; Subfamily mitsporic Pleosporaceae; Genus Alternaria (http://www.uniprot.org/taxonomy/5598). There are 299 species listed in the genus (Kirk et al. 2008); most Alternaria species are saprophytes that are commonly found in soil or on decaying plant tissues (Bart & Thomma 2003). Alternaria fungi proliferation is vegetative in character, and takes place by means of conidial spores, airborne and found in the soil and water, as well as indoors and on objects. Sexual recombination (teleomorphy) occurs very rarely.

Alternaria spp. may be grown on artificial agar media, with PDA (potato-dextrose agar) and V8 (V8 juice - agar) being the most popular in use.
As observed in the in vitro cultures, the pathogens develop fast-growing thick colonies which are usually green-black, or white-gray, with brown to black reverse. Dark septa divide the branched or unbranched conidiophores, carrying the conidial chains. Growing hyphae develop light-brown or dark-tawny, club-shaped spores - single or forming long chains with longitudinal and transverse septa (Fig. 1A).

Primary source of pathogens are the infected seeds or non-decomposed plant debris in the top soil layers with over-wintering hyphae or spores. Another important source of the pathogen are the Brassica weeds, which promote infestations as pathogen host plants (Humpherson-Jones 1989). During the vegetation period, the rain- and wind-transported fungal conidial spores are also an important source of infection. A majority of conidia are released during harvest and cleaning the crops from the infected leaves; such released spores are then spread approximately within 1,800 m (Humpherson-Jones & Maude 1982).

Under Polish climate, highest Alternaria spore concentrations are detected in the air mainly in June and July (Nowakowska et al. 2011).

Alternaria black spot symptoms appear on all host plant parts and at every developmental stage. A. brassicicola and A. brassicae cause the damping off of the crucifers seedlings. Elongated brownings develop on the sub-cotyledonous part of the stem and on the cotyledons, often leading to narrowing and breaking of the stems, and thus, to seedlings' decease. Most often infected are the lower, older leaves of head cabbage (Fig. 1B,C), Chinese cabbage, cauliflower, broccoli, and of other crucifers. Infected cauliflower curds or broccoli florets develop slight dents with brownish spots covered with black bloom of spores. In these plants, infection usually remains on the surface and does not reach deep in the curd or the floret; however, symptomatic cauliflower or broccoli florets lose their commercial value. In case of radish, turnip, or rutabaga, the disease affects the root thickening as well; the disease symptoms manifest themselves as brown rots only during their storage.

Three ways of Alternaria infection have been reported: Through epidermis penetration, through stomata, and through insects- or agrotechnique-derived host plants wounding. Regardless of their means of entry, A. brassicicola and A. brassicae exhibit distinct differences in the host plant tissue penetration. A. brassicae invades host plants solely through their stomata, while for A. brassicicola, direct plant tissue penetration prevails over stomatal infections. Hyphae of both pathogens develop well on the epidermis, directly beneath the leaf waxes, and exhibit low cell penetration ratio. Upon successful pathogen attack, dark-brown spots of different sizes (0.5 cm to several cm in diameter) appear on the leaves; the spots of characteristic concentric circumferences sometimes have a yellow chlorotic halo (Fig. 1B,C). Host plants' reaction to the perceived infection is manifested as almost immediate browning of cell walls, in particular in the parastomatal cells. Under favorable conditions, lesions become covered with brown-black downy-like bloom of sporulating hyphae. A. bras-
sicicola-derived spots are darker and less regular in shape compared with those of A. brassicae origin. As the disease progresses, the spots enlarge, and the infected plant tissue perishes and crumbles, giving rise to dents and hollows (Fig. 1C).

Fig. 1. Alternaria brassicicola and cabbage damping off symptoms. (A) Pathogen mycelium as visible under light microscope [40x]. (B) Characteristic concentric lesions on the abaxial leaf side. (C) Due to heavy infection, seedlings display black spot symptoms, followed by damping off.

Development of the pathogen’s infection structures and of the disease symptoms on the oleraceous Brassicas depends primarily on the incubation temperature (Bassey & Gabrielson 1983), and relative air humidity. While spores of both Alternaria species germinate in a rather broad temperature range, germination effectiveness is correlated with the temperature (Degenhardt et al. 1982). Optimal hyphae growth temperature for A. brassicae is
18-24°C, and for *A. brassicicola* 20-30°C. According to the *in vitro* studies, sporulation of *A. brassicicola* is temperature-dependant: At 8-24°C, fully-developed spores are detectable at 24 or 14 h, respectively. Temperature spectrum of *A. brassicicola* sporulation is broader (8-30°C), with fully-developed spores detectable after 43 or 14 h, respectively. High air humidity (95-100% RH) lasting at least 9-18 h is a crucial requirement displayed by both pathogen species during plant infection (Humperson-Jones & Phelps 1989). Reports of massive infestations under air temperatures of 20-27°C and constant plant moisture of at least 5 h, or RH exceeding 95% lasting at least 12-20 h are commonplace (reviewed in Bart & Thomma 2003).

During plant infection, both *Alternaria* fungi produce and exude phytotoxins that belong to HST clade (host-specific toxins or host-selective toxins; Parada *et al.* 2008, Wight *et al.* 2009). These compounds play a major role in the pathogenesis by determining the host plant spectrum, as well as the isolates’ virulence and pathogenicity levels (Nishimura & Kohmoto 1983). To date, two HSTs have been characterized in detail: AB toxin of *A. brassicicola* (Otani *et al.* 1998) and ABR of *A. brassicicola* (Parada *et al.* 2008). Both phytotoxins are proteins with a suggested role in evoking disease symptoms on the infected cruciferous plants.

In addition to the above, *A. brassicicola* produces a number of phytotoxins (destruxin B and derivatives, such as homodestruxin B, desmethyldestruxin B, and destruxin B₂) responsible for typical black spot symptoms, such as necrotic and chlorotic lesions. Destruxin B was shown to be a major one responsible for inducing necrotic lesions on plant leaves and eliciting the phytoalexins brassilalexin and sinalbin A (Sodelade *et al.* 2012). Majority of researchers classify destruxin B as an HST (Sodelade *et al.* 2012), while others have demonstrated its unspecific character and questioned its role in the initial host plant colonization (Buchwaldt & Green 1992, Parada *et al.* 2008). While some isolates of *A. brassicicola* produce destruxin B as their sole toxin, others are capable of production of their derivatives (homodestruxin B, desmethyldestruxin B, and destruxin B₂; Parada *et al.* 2008).

Depudecin, an eleven-carbon linear polyketide and histone deacetylase (HDAC) inhibitor made by *A. brassicicola*, proved a minor virulence factor. Depudecin-minus mutants have a small (10%) but highly significant (p<0.01) reduction in lesion size on cabbage, but not on *Arabidopsis*, including the pad3 mutants, a susceptible control for *Alternaria* inoculation (Zhou *et al.* 1999, Wight *et al.* 2009). Likely reasons for only a minor role of this polyketide in *A. brassicicola* pathogenicity on cabbage and *Arabidopsis* are: Depudecin concentrations or penetration insufficient to effectively inhibit host plant’s HDAC; HDAC inhibition playing major role in pathogenicity in grasses but not in other plants (cabbage, *Arabidopsis*); redundancy of HDAC inhibitors in *A. brassicicola*, masking the depudecin loss (Wight *et al.* 2009).

*Alternaria* spp. pathogens are also capable of production of other unspecific toxins. In all *Alternaria* - infected organs, alternariol and tenuazonic acid
have been detected. Alternariol-induced cytotoxicity is mediated by activation of the mitochondrial pathway of apoptosis. High concentrations of tenuazonic acid inhibit protein synthesis and, thus, negatively affect seed germination (Tylkowska et al. 2003, Bart & Thomma 2003). Moreover, *A. brassicaceae* and *A. brassicicola* produced cytokines cause green discolorations within the diseased spots (Tylkowska et al. 2004). *A. brassicaceae*-derived abscisic acid causes premature leaf aging and defoliation, dropping flowers, or premature breaking of the siliques (Tewari 1991a).

**Disease impact**

The highest toll the *Alternaria* collect is on the seed plantations of the oleraceous Brassicas, including the cabbages. Infected silique tissue perishes and withers, as a result of which the siliques shrink, break open, and the seeds drop (Maude & Humpherson-Jones 1980), which generates significant economic losses. Upon strong infections of young siliques, the seeds do not develop, or remain underdeveloped, and exhibit decreased vigor and germinability (Chirco & Harman 1979). Infected seeds may display the hyphae present on their surface (surface infection), but the hyphae is able to grow through the seed cover (internal infection). Spores localized both internally and externally may survive several years, although the internal infection seems to be more durable (Maude & Humpherson-Jones 1980). Seedlings developing from infected seeds show typical symptoms of damping off (small black spots on the bottom leaf surface or dark stripes on the hypocotyls).

**Sources of Alternaria spp. resistance**

Brassica crops endangered with *Alternaria* black spot necessitate complex projects on production of varieties with high levels of genetic resistance. An accomplishment of new varieties of these crops exhibiting resistance against the disease is regarded as potentially most economically feasible solution to limiting the yield losses. Such a task remains crucial from the standpoint of the vegetable producers, as well as of the consumers. It allows for a decrease in pesticide use, which is of particular importance in the integrated and ecological vegetable production. Unfortunately, such resistance breeding of the crops is currently hindered due to bottlenecks experienced in transfer of resistance from the wild species into commercial lines.

Until now, no high-level resistance sources against *A. brassicicola* or *A. brassicaceae* have been identified among the cultivated species of the *Brassica* genus; however, individual varieties among the cabbages may differ in the exhibited levels of susceptibility to black spot (Otani et al. 2001). The highest level of *Alternaria* resistance from among the *Brassica* crops is displayed by the Ethiopian mustard (*B. carinata*). Among the wild cruciferous plants closely related to the *Brassica* genus, the highest *A. brassicaceae* resistance levels were confirmed for white mustard (*Sinapis alba*; Kolte 1985, Brun et al. 1987, Ripley et al. 1992, Sharma & Singh 1992, Hansen & Earle 1995, 1997); however, the highest overall *Alternaria* spp. resistance has been identified in the crucifers species more distant from the *Brassica*, such as camelina (*Came-
**lina sativa;** false flax), shepherd's-purse (Capsella bursa-pastoris), rucoila (Eruca sativa), and ball mustard (Neslia paniculata) (Conn & Tewari 1986, Conn et al. 1988, Tewari 1991b). Resistance against Alternaria black spot has also been reported among other wild members of the Brassicaceae family (Sharma et al. 2002, Tewari & Conn 1993; reviewed and referenced in Warwick 2011): Alliaria petiolata; Barbarea vulgaris; Brassica elongate, B. desnottessi, B. fruticulosa, B. maurorum, B. nigra, B. souliei, B. spinescens; Camelina sativa; Capsella bursa-pastoris; Coincya spp.; Diplotaxis catholica, D. berthaultii, D. creacea, D. erucoides, D. tenuifolia; Erucastrum gallicum; Eruca vesicaria subsp. sativa; Hemicrambe fruticulosa, H. matronalis; Neslia paniculata; Raphanus sativus; S. alba, and S. arvensis. The completely-immune plants remained symptom-free both, under natural field infection, as well as under controlled artificial inoculation (Sharma et al. 2002). Comparatively, broccoli and cauliflower varieties exhibited only moderate Alternaria resistance, while the cabbages turned out susceptible.

**Resistance background**

Depending on the plant material studied, A. brassica/A. brassicicola resistance was said to be controlled by one or several nuclear genes of partially-dominant interaction (Zhang et al. 1997) or is conditioned by additive inheritance (Krishnia et al. 2000). On the biochemical level, resistance against Alternaria pathogens seems to be connected with high activities of phenolases (polyphenol oxidase, peroxidase, catalase), high levels of leaf sugars (Singh et al. 1992), and thicker epicuticular wax layer forming a hydrophobic coating to reduce the adherence of water-borne inoculum, as well as limiting spore germination rate (Meena et al. 2010). Presence of intensive leaf wax deposition seems correlated with the resistance exhibited by other Brassicaceae plants (Meena et al. 2010).

Wild crucifers are found to elicit phytoalexins upon challenge inoculation (Conn et al. 1988). Among the Alternaria-resistant species, camelina stands out for its immunity against A. brassicicola infection, originating in the plant’s ability to synthesize camalexin, a compound with antibiotic properties, and thus to hamper pathogen’s development. Indeed, it has been demonstrated that camalexin deficient Arabidopsis mutant, pad-3 is more susceptible to A. brassicicola than wild-type plants (Zhou et al. 1999). Additional evidence that camalexin plays a major role in resistance came from the observation that different Arabidopsis ecotypes with varying levels of camalexin show correlative differential resistance (Kagan & Hammerschmidt 2002). Finally, the esa1 mutation affects resistance against A. brassicicola through a severe reduction in both camalexin production, as well jasmonate-depen-dent gene induction, although the Esa1 gene has yet to be cloned (Tierens et al. 2002).

**Resistance testing**

A direct method of determination of Alternaria resistance are the phytopathological tests: Field-, greenhouse-, or phytotron-based. Field observations can be carried out upon natural pathogen infection, or after controlled artificial inoculation with fungal spore
suspension. Advantages of the greenhouse or phytotron tests are: Speediness, reproducibility, and a possibility of control of the conditions. Phytopathological tests require *Alternaria* spp. conidia, collected directly from the infected plant tissue or maintained on the artificial media. On the commonly used PDA artificial media, fungal growth and effective spontaneous sporulation take place at 25±2°C, in darkness. A choice of other methods exist towards *Alternaria* spp. growth and maintenance. *A. brassicicola* hyphae has been successfully cultured on artificial media V8A (V8 juice - agar) at 25°C, resulting in spontaneous sporulation under 12 h photoperiod (Otani et al. 1998).

Controlled-conditions phyto-tests are carried out on whole plants (*in vivo*) or on detached leaves (*in vitro*; Sharma et al. 2002). Plants are routinely tested at 3-6 weeks seedlings stage, but cotyledon phyto-tests have been published as well (Doullah et al. 2006). The detached leaf method is one of the most often employed ways to assess the *Alternaria* spp. resistance levels displayed by the tested plants under controlled conditions. Differences exist, however, regarding the inoculation method and assay conditions. As described in several studies, inoculum of 5×10^4 spores×ml⁻¹ was placed at the upper (adaxial) leaf side (Doullah et al. 2006), while other authors described spraying the lower (abaxial) leaf side with inoculum of 3×10^5 spores×ml⁻¹ (Parada et al. 2008). Yet others inoculated only the 4th and 5th leaves (seedling 45 days old; Sharma et al. 2002). Wet swabs have been used to remove the leaf wax layers on both nerve sides on the adaxial leaf surface, due to which the aqueous spore suspension gets uniformly distributed on the leaf surface, without the need of adding agar or adjuvants (Sharma et al. 2002). Better adhesion of the water-suspended spores to wax-covered leaf surface of cabbages is granted by addition of agar (Ho et al. 2007) or Tween (Doullah et al. 2006). Thin needle has been employed to make small surface cuts, onto which a droplet of inoculum (4×10^3 spores×ml⁻¹) was placed.

Disease symptoms have been scored in 24 h increments for 3 dpi. Resistance scoring of individual plants included three parameters: Percentile of infected leaf surface (0-60 pts), lesion size (0-30 pts), and incubation duration (0-10 pts). Plants exhibiting maximum susceptibility scored 100 points. Individual plants have been grouped into the resistance classes, according to their points scoring: 0-fully resistant; 1-15 pts – moderately resistant; 16-25 pts – susceptible; above 25 pts – highly susceptible. As discussed above, optimal phyto-test conditions are temperatures of about 20°C, relative humidity of at least 90% lasting for 6 h and more, and inoculum load of 6×10^4 spores×ml⁻¹ (Sharma et al. 2002, Doullah et al. 2006).

**Bottlenecks in resistance breeding**

Since resistance against *Alternaria* black spot is generally governed by polygenes, breeding for resistance could involve pyramiding of minor genes to provide additive/polygene resistance. Rapid advances in techniques of tissue culture, protoplast fusion, embryo rescue, and genetic engineering have made possible the transfer of disease resistance traits
across the otherwise impassable self-incompatibility barriers. Transgenic plants with disease resistance which over-express different antifungal compounds like pathogenesis-related (PR) proteins (chitinase, glucanase, osmotin, etc.) and ribosome inhibiting proteins (RIPs) such as thionins, defensins, and phytoalexins (Zhou et al. 2002) to inhibit growth of the pathogen, seem less efficacious.

To introduce camelina-derived *A. brassicicola* resistance into commercial varieties, somatic hybrids between *C. sativa* and *B. carinata* have been procured; however, the researchers failed to multiply the resulting hybrids (Narasimhulu et al. 1994). Similar strategy of protoplast fusion between *C. sativa* and *B. oleracea* with subsequent hybrid regeneration also proved unsuccessful (Hansen 1998). Several research groups attempted, but not succeeded, to introduce the *E. sativa*-deriving *black spot* resistance into various species of cultivated crucifers (Fahleson et al. 1988, Sikdar et al. 1990, Sigareva & Earle 1997). The first somatic hybrids to be obtained as a result of protoplast fusion were those of *B. napus* (rapeseed) and *S. alba* (Primard et al. 1988). None of the hybrids procured that way showed *A. brassicaceae* resistance comparable to that exhibited by *S. alba*. Chevre et al. (1991) used these species towards interspecies crosses through somatic hybridization and bidirectional crosses. Having employed the embryo rescue technique, the researchers succeeded in regeneration of *B. napus* plants carrying 38 chromosomes typical for that species, and displaying *A. brassicaceae* resistance at levels close to this of *S. alba*, *B. oleracea* var. *botrytis*, or *B. carinata* (Ryschka et al. 1996). Seeds of developed intertribal somatic hybrids between *B. napus* and *C. sativa* (by means of protoplast electrofusion) exhibited phenotype intermediate compared with the parental species. They also exhibited higher level of linolenic and eicosanoic acids, but the hybrid plants await determination of their *Alternaria* resistance (Jiang et al. 2009).

In general, it has been postulated, that introduction of *Alternaria* resistance genes into commercial cultivars of crucifers is dependent on cumulation of horizontal resistance genes (Sharma et al. 2002). Hence, it is imperative to identify various sources of horizontal resistance among the *Brassica* plants (see above), and subsequently to combine them towards increase in durable *Alternaria* protection. Strong cross-incompatibility, polygenic background of the resistance (additive and dominant gene interactions), as well as the differences in ploidy (differing number of chromosomes) between respective *Brassicaceae* species render the transfer of *Alternaria* resistance from the wild species into the cultivated forms difficult. Additionally, it is often connected with employment of advanced *in vitro* hybridization techniques, including somatic hybridization, embryo and ovary rescue, or protoplast fusion.

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ALTERNARIOZA ROŚLIN KAPUSTOWATYCH: OBJAWY, SZKODLIWOŚĆ I PERSPEKTYWY HODOWLI ODMIAN ODPORNYCH

Streszczenie

Alternarioza kapustowatych (syn. czerń krzyżowych, czarna plamistość roślin krzyżowych) powoduje duże straty gospodarcze w wielu krajach, w tym również w Polsce. Sprawcami choroby są różne gatunki grzybów z rodzaju *Alternaria*, najczęściej: *A. brassicae* (Berk.) Sacc., *A. brassicicola* (Schw.) Wiltsh., *A. raphani* Groves i Skolko oraz *A. alternata* (Fr.) Kreissler. Roślinami żywicielskimi są kapusty i inne rośliny uprawne oraz dziko rosnące z rodziny krzyżowych. Szkodliwość czerń krzyżowych w uprawie kapusty głowiastej i pekińskiej polega na obniżeniu wysokości i jakości plonu. Grzyby z rodzaju *Alternaria* wywołują również zgorzel siewek, zgorzel podstawy główek kapusty, brązowienie róż kalafiory oraz brokulu. Najczęściej porażane organy wegetatywne roślin kapustowatych są infekowane przez *A. brassicicola* i *A. brassicaceae*, natomiast w uprawie nasiennych roślin oleistych w obrębie rodzaju *Brassica* dominującym sprawcą alternariozy jest *A. brassicaceae*. Pierwotnym źródłem choroby są głównie zakażone nasiona, ale także zimotwarte rośliny z rodziny krzyżowych, resztki porażonych roślin, a na plantacjach nasiennych również materiał wysadkowy.
Metody zapobiegania i zwalczania alternariozy na plantacjach polegają na łączeniu zabiegów agrotechnicznych z ochroną chemiczną. Podstawową metodą zapobiegania chorobie jest produkcja zdrowych nasion, które otrzymuje się, stosując systematyczne opryskiwanie plantacji nasiennych fungicydami. W pierwszym roku uprawy zwalczanie ogranicza się do przedsiewnego zaprawiania nasion, a w czasie wegetacji, w okresach wzmoconego zagrożenia chorobą, znaczne obniżenie porażenia uzyskuje się dzięki regularnym opryskom środkami grzybobójczymi. Według wielu autorów, najbardziej ekonomicznym rozwiązaniem byłoby uzyskanie odpornych odmian warzyw kapustowatych. Pozwoliłoby to na zmniejszenie zużycia pestycydów, co ma szczególne znaczenie w uprawach integrowanych i ekologicznych. Pomimo identyfikacji źródeł odporności wśród roślin z rodziny krzyżowych, przeniesienie tej cechy do uprawnych gatunków kapustowatych jak dotąd nie powiodło się.

Silne bariery niezgodności krzyżowej, poligeniczne uwarunkowanie odporności (addytywne i dominujące współdziałanie genów) oraz różnice w ploidalności pomiędzy poszczególnymi gatunkami rodziny krzyżowych sprawiają, że przeniesienie genów odporności z dzikich gatunków do form uprawnych jest bardzo trudne i wymaga wykorzystania technik hybrydyzacji in vitro (w tym: somatyczna hybrydyzacja, „embryo/ovary rescue”, fuzja protoplastów). Jednak dzięki coraz lepszemu poznaniu wzajemnych relacji patogen-rosлина żywicielska, identyfikacji nowych źródeł odporności oraz określeniu mechanizmu dziedziczenia tej cechy, możliwy będzie postęp w hodowli roślin kapustowatych odpornych na alternariozę.