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Journal of Invertebrate Pathology 92 (2006) 125–131
Journal of INVERTEBRATE PATHOLOGY
www.elsevier.com/locate/yjipa

Factors affecting transmission of fungal pathogens of aphids

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Received 28 February 2006; accepted 20 March 2006
Available online 14 June 2006

Abstract

Fungal pathogens are the most important pathogens of aphids (Homoptera: Aphididae), and epizootics, particularly those caused by Entomophthorales (Zygomycota), are frequently observed and often rapidly reduce aphid populations. Fungi in the Hypocreales (Ascomycota) are less commonly found infecting aphids but can be important. The transmission of aphid fungal pathogens is affected by many factors, including: host biology and structure, pathogen characteristics, host-plant characteristics, and environmental factors. This paper is an overview of selected factors affecting transmission of aphid pathogens.

Keywords: Aphididae; Fungi; Entomophthorales; Dispersal; Epizootics

1. Overview of aphids and their pathogens

Aphids (Homoptera: Aphididae) are among the most successful families of insects and many are serious agricultural pests (Kennedy and Stroyan, 1959; Sorensen, 2003). Aphids feed on phloem sap via extremely fine maxillary stylets that penetrate phloem sieve tubes, greatly reducing the possibility that aphids will ingest viruses, bacteria, or protozoa on plant surfaces. Therefore, fungi are the most important microbial pathogens of aphids because fungi can infect through the integument. At least 16 species of fungi are known to naturally infect aphids, and several species frequently cause epizootics in aphid populations (Gustafsson, 1965; Thoizon, 1970; Bałazy, 1993; Keller, 1991, 1997).

Most aphid-pathogenic fungi are in the Entomophthorales (Zygomycota), however, several Hypocreales (Ascomycota) genera, such as *Beauveria*, *Verticillium*, and *Paecilomyces*, are also known to infect aphids (Milner, 1997). The most common species of Entomophthorales causing epizootics in aphids are: *Pandora* (=*Erynia*) *neoaphidis*, *Neozygites fresenii*, and *Entomophthora planchoniana*. *Conidiobolus obscurus*, *Zoophthora kondoiensis*, *Z. erinacea*, *Z. aphidis*, *Z. anhuiensis*, *Z. phalloides*, *N. microlophii*, *N. lageniformis*, *N. turbinata*, and others are also encountered, although less commonly.

Epizootics in aphids caused by fungi are common (Pell et al., 2001), and *P. neoaphidis* is considered the most common causative agent of epizootics (Nielsen et al., 2003). It has been recorded from >70 species of aphids (Pell et al., 2001). For example, MacLeod (1955) collected *Macrosiphum pisi* from an orchard in Nova Scotia, Canada, and found that 76.1% were infected with *P. neoaphidis* ($n = 3822$). MacLeod et al. (1976) reported that *E. planchoniana* destroyed an *Aphis rumicis* population in England and the same fungus killed 88% of walnut aphids, *Chromaphis juglandicola*, in walnut groves in California. McLeod et al. (1998) reported epizootics caused by *P. neoaphidis* in *Myzus persicae* populations on spinach, *Spinacia oleracea*, in Arkansas. Widespread epizootics caused by *N. fresenii* have occurred with great regularity in cotton aphid (*Aphis gossypii*) populations in the United States (Hollingsworth et al., 1995) and in Africa (Silvie and Papierok, 1991).

Transmission is a key ecological factor that must be understood before entomopathogens can be manipulated. "Understanding the mechanisms of transmission of a given entomopathogen will allow prediction of its ability to spread within a host population and, in some cases, of its potential as an applied microbial control agent"

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0022-2011/$ - see front matter © 2006 Elsevier Inc. All rights reserved.
doi:10.1016/j.jip.2006.03.009

(Harper, 1987). According to Hajek and St. Leger (1994): "dispersal of infective propagules to a new host represents a most perilous part of the fungal life cycle. Processes of spore production and discharge, spore dispersal, and spore survival and germination frequently depend on environmental conditions." The factors that affect transmission of aphid pathogens are diverse and may be divided into four broad categories: host-related factors, pathogen-related factors, host-plant-related factors, and environmental factors.

2. Effect of host-related factors on transmission

2.1. Effect of aphid biology and morphology on transmission

Insects and other arthropods differ widely in their biologies, feeding habits, habitats, and morphologies; factors that may determine which pathogen groups most commonly infect hosts. Aphids are a good example of a taxon that is successfully exploited by entomopathogenic fungi. Many aphid characteristics play a role in the development of fungal epizootics. Aphids are small, soft-bodied hemimetabolous insects with rapid life cycles, relatively short life spans, often parthenogenetic and viviparous, and they produce both wingless (apterous) and winged (alate) morphs. Aphids are phloem feeders and possess fine stylets for piercing host-plant tissues (Miyazaki, 1987).

Because aphids are hemimetabolous the larvae (nymphs) live and feed in colonies with the adults, resulting in the entire population being susceptible to attack by fungal pathogens (Fig. 1). This is in marked contrast to pathogen dynamics in insects such as Hymenoptera, Lepidoptera, Diptera, and other holometabolous insects in which entomopathogens are usually restricted to either the larval or adult stage.

Aphids are often parthenogenetic for much of their life cycle, producing aphid colonies made of genetically identical clones. Therefore, all the aphids in a colony may be relatively equal in susceptibility to a pathogen. Characteristics such as parthenogenesis, short life cycles, and viviparity during most of the life cycle lead to very rapid population increases under suitable conditions. Dense populations of aphid nymphs and adults often result through which fungal pathogens can rapidly spread (Figs. 1 and 2).

Feeding by fine maxillary stylets appears to be the major factor that reduces exposure of aphids to viral, protozoan, and bacterial pathogens. The small soft (weakly sclerotized) bodies of aphids also appear to present relatively few barriers to penetration by fungal pathogens specialized for infection of aphids. The small size of aphids may also be related to the relatively short time required for some fungal pathogens to kill the host. Cotton aphids infected with *N. fresenii* died within 3–4 days after infection at 25–30 °C (Steinkraus et al., 1993). Other fungal pathogens have more typical incubation periods, for example, Dromph et al. (2002) found LT_{50} values for *Sitobion avenae* infected with *P. neoaphidis* were between 6.5 and 7.5 days.

2.2. Effect of aphid morph on transmission

Production of apterae and alatae (Fig. 3) affects the transmission of fungal pathogens. The importance of infected alatae (Figs. 3 and 4) in transmission and dispersal of aphid pathogenic fungi has been demonstrated by studies in China. Feng et al. (2004) trapped alate aphids from >30 m above ground and found that 36.6% of 7139 migratory alatae of eight different aphid species were infected with fungal pathogens. Over 90% of the fungal pathogens were Entomophthorales, including *P. neoaphidis* (69%), *E. planchoniana* (12%), *B. bassiana* (9%), *C. obscurus* (5%), *Z. anhuiensis* (4%), *Z. radicans* (4%), *Paecilomyces* sp. (<1%), and *N. fresenii* (<1%).

In a study of susceptibility of different color morphs of apterae and alate *S. avenae* to *P. neoaphidis*, Dromph et al. (2002) found that LC_{50} values for both green and brown alatae were lower than those for apterae. The higher susceptibility of alatae is important because infected alatae fly and disperse fungal pathogens between fields and can initiate dispersal from aphid colonies on winter hosts to cereal fields (Dromph et al., 2002). Clearly the higher susceptibility of alatae and their ability to fly long distances when infected are important factors in development of epizootics (White et al., 2000).

3. Effect of pathogen-related factors on transmission

Different pathogen groups and species have various strategies for infection, dispersal, and survival. Detailed studies on individual pathogen species and their hosts are required for understanding transmission. Pathogen-related factors include active or passive discharge of conidia, conidial size, shape and number, attachment mechanisms, and survival mechanisms.

3.1. Conidial discharge, size, and characteristics

Most of the fungal species causing epizootics in aphids are in the Entomophthorales, which are characterized by forcibly discharged primary conidia; important in both short- and long-range dispersal of the entomophthoralean pathogens. Conidia in the Hypocreales such as *B. bassiana* or *V. lecanii* are passively dispersed.

Another difference between the Entomophthorales and Hypocreales is conidial size. Entomophthoralean conidia usually are large, 15–40 μm in diameter compared to Hypocreales (*Beauveria* conidia ca. 3.5 μm in diameter, *Paecilomyces* ca. 3 μm and *Verticillium* ca. 2–10 μm long) (Humber, 1997). Size of conidia may affect the number of conidia needed to infect a host. One capilliconidium of *N. fresenii* is often sufficient to infect a host (D.C. Steinkraus, unpublished data), possibly because more resources are available to a large spore for penetration of the host's integument.

The number of conidia produced per infected host varies based on pathogen species and host size. Glare et al. (1986) found that up to 40,000 conidia of *Z. phalloides* were pro-