



Review

Nosema pyrausta: Its biology, history, and potential role in a landscape of transgenic insecticidal crops

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ABSTRACT

Nosema pyrausta, an entomopathogenic microsporidium, is an important population regulator of the European corn borer, *Ostrinia nubilalis*. This manuscript is a review of research on the relationships between *N. pyrausta* and *O. nubilalis*. *N. pyrausta* was described from *O. nubilalis* in Hungary in 1927 and from *O. nubilalis* in IA in 1950. It affects the basic biology of *O. nubilalis* by slowing larval development, reducing percentage pupation, and decreasing adult longevity, oviposition and fecundity. Infections are maintained in a population by vertical and horizontal transmission. Success of vertical transmission depends on intensity of infection. Horizontal transmission is dependent on stage of larval development at time of infection, quantity of inoculum, and host density. Abiotic and biotic factors coupled with *N. pyrausta* usually have an additive effect in decreasing the fitness of *O. nubilalis*, i.e., cold temperatures reduce fecundity and increase larval mortality, host plant resistance reduces the number of larvae per plant. Also, microbial and chemical insecticides are more effective in reducing plant feeding if the insect is infected with *N. pyrausta*. Predators in general feed on *N. pyrausta*-infected *O. nubilalis* with no decrease in fitness. Parasitoids do coexist with *N. pyrausta*, however, parasitoid fecundity is usually reduced when developing in a *N. pyrausta*-infected host. Previously unreported data are presented on the prevalence of *N. pyrausta* in *O. nubilalis* populations from many parts of the US. These data demonstrate that *N. pyrausta* continues to be present and fluctuate in populations of *O. nubilalis* as it has since its discovery in the US. Also, the dynamics of its presence remain similar through changes in corn production including crop rotations, reduced tillage and transgenic insect-resistant varieties.

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1. Introduction

Nosema pyrausta (Microsporidia: Nosematidae) is an obligate intracellular parasite. As with many other Microsporidia, *N. pyrausta* principally infects a single host species with a few exceptions. In this case, the host is the European corn borer, *Ostrinia nubilalis* (Hübner) (Lepidoptera: Crambidae), a polyphagous crop pest. Because most research on *N. pyrausta* has been based on the pathogen's role in helping regulate *O. nubilalis* populations, an understanding of *O. nubilalis* history and biology helps place information about the pathogen in an appropriate context.

1.1. *Ostrinia nubilalis*—Biology/history

Ostrinia nubilalis was introduced at least twice to the US in the early 1900s, most likely in shipments of broom corn from Hungary and Italy. It was first reported in Boston, MA in 1917 (Caffrey and Worthley, 1927). Over the next several years it spread westward to NY, PA, OH and MI (1919–1921), WI (1938), IL (1939), IA (1942), NE (1944) and SD (1946). *O. nubilalis* has continued to spread where corn is grown, producing a current range which includes all areas of the US east of the Rocky Mountains and north to Canada. Across this range, *O. nubilalis* may be univoltine (northern US and Canada), bivoltine (most of the US Corn Belt), or multivoltine (three to four generations along the Atlantic Coast and westward to the Gulf States) (Mason et al., 1996). In addition, there are two pheromone races of bivoltine *O. nubilalis*, designated as Z (throughout North American range) or E (eastern US only) race based on preponderance of *cis*- to *trans*-11-tetradecenyl acetate, respectively, in the pheromone blend (Cardé et al., 1975). There is partial reproductive isolation between the univoltine and

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bi/multivoltine races, and between the Z and E pheromone races (Roelofs et al., 1985).

Corn, *Zea mays* L. (Poales: Poaceae), is the primary host plant of *O. nubilalis*, however, this insect has been collected from over 200 plant species ranging from ornamentals to cultivated crops such as oat and sorghum (Hodgson, 1928). Although *O. nubilalis* has been collected from numerous plants, there are empirical data documenting development from larva to adult on but a few species. Economic damage routinely occurs on corn, sorghum, green beans, pepper and potato. However, most field research has been conducted on *O. nubilalis* as a pest of corn.

In Iowa, the state leading in corn production, *O. nubilalis* is a bivoltine insect. Adults eclose from pupae that overwintered as last instars in crop residue. In mid May to early June adults lay eggs on vegetative-stage corn, larvae eclose, move into the whorl of the plant and feed at the leaf-moisture interface where the leaves are unfurling, resulting in characteristic shot-hole pattern of damage in the leaves. The late 4th to early 5th instars bore into plant stalks, pupate and emerge as second generation adults. These adults lay eggs primarily on the underside of corn leaves of early to mid reproductive-stage plants. Neonates feed on pollen concentrated at the leaf-axil/stalk juncture. Initial plant feeding occurs behind the sheath collar and leaf ribs and again late 4th to early 5th instars bore into the stalk. Larvae tunnel extensively, enter diapause and pass the winter, breaking diapause to pupate and eclose as adults in spring of the following year.

1.2. Management

After the introduction of *O. nubilalis* there were many efforts to eradicate it using primarily cultural control methods (burning plant residue and plowing under corn stalks) as well as quarantining infested areas. After quarantine efforts failed, crop protection became the primary concern; arsenicals and nicotine-based products were used initially followed by nearly all classes of synthetic chemical insecticides applied to corn as they came on the market. Microbial insecticides, primarily *Bacillus thuringiensis*-based products with an occasional *Beauveria bassiana*-based product were used in the 1970s, 1980s and 1990s as crop protectants. Commercial use was restricted mostly to managing *O. nubilalis* in production of organic commodities and in hybrid seed production. Concurrently, much emphasis was placed on host-plant resistance. Thousands of maize cultivars were screened to identify those resistant/tolerant to *O. nubilalis* whorl feeding. The hydroxamic acid DIMBOA was identified as the component of antibiosis in some inbred lines of corn. Working with corn breeders, entomologists developed lines of corn that produced DIMBOA along with other desirable agronomic traits (Klun et al., 1970). Entomologists and plant breeders have identified germplasm with resistance to sheath-collar feeding, a characteristic desirable in reproductive-stage plants for insect resistance; however, these sources were not readily available in Corn Belt germplasm, and the identification process was more laborious than identifying resistance to whorl feeding. Thus, progress developing hybrids with sheath-collar resistance has been slower. Even so, a large percentage of commercial hybrids have some resistance to feeding by *O. nubilalis* during the reproductive stage of the plant (Barry and Darrah, 1991). In the late 1990s the era of genetically modified (= transgenic) corn was ushered in, creating plants that were insecticidal throughout the growth period (Kozziel et al., 1993). The first transgenic plant product to reach the market was corn expressing the insecticidal protein Cry1Ab from *B. thuringiensis* (Bt). After an initially slow adoption of transgenic technology, growers became more accepting of this “built in” insecticide, and now 49% of the US Corn Belt is planted with Bt corn (USDA-ERS, 2006).

2. Nosema pyrausta

2.1. History and biology

The earlier literature (prior to 1975) on the microsporidiosis in *O. nubilalis* refers to the causative organism as *Perezia pyraustae*; after 1975 the organism is most often referred to as *N. pyrausta*. The microsporidium from *O. nubilalis* was described in 1927 as *Perezia pyrausta* (Paillot, 1927); and later Paillot (1928) again described this microsporidium spelling the specific name as *pyraustae*. Because Paillot originally published the specific name as *pyrausta* it took precedence over *pyraustae*. Subsequently *Perezia* was declared an invalid genus, and was replaced with *Nosema*. More recently, molecular analysis has confirmed the identification of the microsporidium as *N. pyrausta* and its close phylogenetic relationship to the *Vairimorpha* species (Baker et al., 1994; Vossbrinck and Debrunner-Vossbrinck, 2005). This microsporidium was isolated from *O. nubilalis* larvae collected from IA and OH in 1950 (Steinhaus, 1952), and its identity was confirmed as *Perezia pyraustae* by Hall (1952) using the caterpillar *Junonia coenia* Hübner (Lepidoptera: Nymphalidae) as a surrogate insect. The name *N. pyrausta* was first used in the literature by Lewis and Lynch (1974). *O. nubilalis* is the only lepidopteran reported to be infected in nature with *N. pyrausta*.

Nosema pyrausta has an infection cycle similar to most microsporidia, i.e., once a *N. pyrausta* spore is consumed by an *O. nubilalis* larva, the spore's polar filament is extruded, penetrating a midgut cell and inoculating it with sporoplasm. The sporoplasm undergoes the vegetative developmental stages of merogony, schizogony, and sporogony giving rise to several additional spores. Once an infection has been established within an insect, infected cells can rupture spreading the infection internally. Malpighian tubules, midgut cells, silk glands, reproductive tissues and fat body are the tissues most often and most heavily infected (Kramer, 1959).

The effects of *N. pyrausta* on *O. nubilalis* are generally chronic and debilitating but usually not lethal. If the insect has the appropriate food, water and environmental conditions an infection results in few apparent adverse effects. However, when effects do occur they are exhibited in all life stages (eggs, larvae, pupae, and adults) with the magnitude dependent on life stage, instar in which the insect became infected, and the inoculum dose. These effects will be discussed relative to per os or horizontal transmission, and transovarial or vertical transmission. One must, however, be cognizant that the two methods of transmission are closely linked; when both occur they maximize maintenance of *N. pyrausta* in a population.

There are several studies in which horizontal transmission has been quantified, evaluated, and influencing factors defined. In general, horizontal transmission is the process of an insect obtaining an infection in the larval stage by consuming an inoculum while feeding. Horizontal transmission usually results in an increase in the percentage of individuals in a population infected with *N. pyrausta*, as well as an increase in the intensity of infection within individuals. An increased intensity of infection within an individual may be caused by consumption of additional spores, and by initial spores completing a reproductive cycle and generating new ones. Ostensibly, this phenomena also occurs in a vertically-transmitted infection. The rate of horizontal transmission is governed by the percentage of a population infected, time in an instar, mortality, and by proclivity of the microsporidium to vertically transmit. As mentioned earlier, in most of the US Corn Belt, *O. nubilalis* has two generations per year, with the first initiated by moths resulting from overwintered larvae. In this generation the larval stage lasts approximately 20–25 days with feeding primarily in the whorl with little time spent actually being a borer, i.e., making tun-

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