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The host and geographical range of the grasshopper pathogen Paranosema (Nosema) locustae revisited

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Abstract

Host and geographical ranges are updated for the microsporidium Paranosema locustae; this pathogen was developed in the USA as a long-term microbial control agent of grasshoppers. Currently known to be susceptible to P. locustae, either naturally or experimentally, are 121 species of Orthoptera from North and South America, Africa, Australia, China, and India. Most belong to the Acrididae (112), and within this family, to the Melanoplinae (36), Oedipodinae (35), and Gomphocerinae (35). The host range of P. locustae, as presently understood, is based largely on morphology and could change if molecular techniques reveal cryptic species. The North American isolate is not only the best studied, but the one established after its introduction into Argentina, and produced and used in China: it can be considered a generalist pathogen. As such, P. locustae may have the ability to alter, through differences in host susceptibilities, the structure of grasshopper assemblages in areas where it was not present before. Long-term careful monitoring of key grasshopper species in areas of pathogen introduction/establishment may reveal such effects.

Introduction

Paranosema locustae is a spore-forming pathogen of the adipose tissue of orthopterans that was isolated, selected, and developed in the USA as a long-term microbial control agent of grasshoppers (Henry & Oma 1981, Johnson 1997, Lockwood et al. 1999). P. locustae belongs to the Microsporidia, a group of unicellular eukaryotes that are obligate intracellular parasites of animals and some protists (Wittner & Weiss 1999). Microsporidia were historically regarded as Protozoa or Archezoa, but recent studies at the molecular level have shown they are actually related to Fungi (Keeling & Fast 2002).

In North America, Steinhaus (1951) first noticed P. locustae, albeit without naming it, in 3 species of grasshoppers of the genus Melanoplus from Montana. Soon after, Canning (1953) described P. locustae as Nosema locustae, using diseased African migratory locusts, Locusta migratoria migratorioides, from a rearing colony at the Imperial College Field Station in London. Sokolova et al. (2003), while erecting the new genus Paranosema for another microsporidian pathogen of Orthoptera from the cricket Gryllus bimaculatus, transferred N. locustae to Paranosema, based on molecular and ultrastructural grounds, erecting the new combination P. locustae. Even more recently, Slamovits et al. (2004) proposed another new combination, Antonospora locustae; but Sokolova et al. (2005) provided reasons for favoring the name P. locustae.

One of several factors that permitted the selection of P. locustae for its development as a microbial control agent, is its wide host range among acridomorphs. While the host range of most Microsporidia is relatively narrow (Solter et al. 2005), host specificity is a species-based character in Microsporidia, that should be considered individually (Solter & Becnel 2003). The unusually broad host range of P. locustae was observed early in its development as a biocontrol agent (Henry 1969), and judged to be desirable (Henry 1977). This was because many grasshopper species are considered pests, and frequently, when outbreaks occur, more than one (and sometimes several) species are involved.

Henry (1969) provided the first list of hosts that he knew to be susceptible, which included 55 North American species, 53 of them acridomorphs, one cricket, and one tetrogid. Almost 2 decades later, Brooks (1988) presented a new list of worldwide susceptible insects, all of them Orthoptera, expanding the known host range of P. locustae to 95 species. Since then, additional work has been conducted on P. locustae, much of it outside of North America, in Argentina, China and South Africa. The present update compiles the current available knowledge on the host and geographical range of P. locustae. Caution should be exerted when assessing the currently known host range of P. locustae because it is largely based on morphological grounds. The possibility that a scrutiny of different isolates at the molecular level could reveal the occurrence of cryptic species cannot be ruled out.

Host range and distribution

Table 1 shows, by continent, family, and subfamily, all the species reported to be susceptible, either naturally or experimentally, to P. locustae, which at present total 121. Of these, 112 species are Acrididae, and the remaining 9 susceptible species belong to the families Romaleidae (3), Gryllidae (1), Oecanthidae (1), Tettigidae (1), Tettigonidae (1), and Pyrgomorphidae (2). Among the Acrididae, susceptible species are in the subfamilies Acridinae (2), Calliptaminae (1), Catantopinae (2), Cyrtacanthacridinae (5), Copiocerinae (1), Eyprepocnemididae (3), Gomphocerinae (23), Melanoplinae (36), Oedipodinae (35), Oxyinae (3), and Tropidopalinae (1). Based on the host species involved in the natural infections (ecological host range, Solter et al. 2005), on the natural and induced (after field applications) prevalences, the results of laboratory bioassays (physiological host range, Solter et al. 2005), and on the intensity of infections (spore loads per individual), it appears that species in the subfamilies Melanoplinae, Oedipodinae, and Gomphocerinae are generally more susceptible than species in other subfamilies (Canning 1953; Henry 1969; Henry et al. 1973; Ewen 1983; Lockwood 1988; Whitlock & Brown 1991; Bomar et al. 1993; Wang & Yu 1994; Yuhua 1997; Lange 2003 a, b). It is important to note that in the earlier literature on host range of P. locustae (Henry 1969), most species that by then were treated as Cyrtacanthacridinae are now considered to be within the Melanoplinae.
P. locustae has been reported to be native in North America, India and South Africa (Henry 1969, Ewen 1983, Srivastava & Bhanotar 1985, Raina et al. 1987, Whitlock & Brown 1991). It has been mentioned for the Irkutsk region of Russia (Issi & Lipa 1968), but has later apparently treated by Issi & Krylova (1987) as a different species, Nosema chorthippi. However, aside from the original description by Canning (1953), virtually all available knowledge on P. locustae comes from research on the North American isolate, while the records for India were poorly diagnosed.

The North American isolate of P. locustae has become established after its introduction in the Pampas of Argentina (Sokolova & Lange 2002, Lange 2003a, Lange & De Wysiecki 2005), and it is produced and used in China for the control of grasshoppers and locusts (Long 1995, Wangpeng et al. 2001, Shi & Nijaqi 2004). Unfortunately, the fate of introductions conducted in other countries, such as Australia, Cape Verde, Mali, Niger, and Mauritania has not been explored.

The present update shows the significant, relatively recent, expansion in host and geographical ranges of P. locustae, mostly as a result of applied use. Due to the extremely wide host range acknowledged at present for P. locustae, this microsporidium clearly qualifies as a generalist pathogen. In assessing the significance of this, those infections recorded in field-collected individuals, either naturally (labeled as N in Table 1), or as induced infections following an introduction or augmentation event (labeled as I and A in Table 1), are of particular relevance. Although the physiological host range can be used as an indicator of ecological host range, it needs to be carefully observed and evaluated. When forced into experimental hosts during bioassays, some microsporidia are known to develop atypical infections that are not likely to occur or persist in the field (Solter et al. 2005).

A generalist pathogen has the ability to alter, through differences in host susceptibilities, the structure of insect assemblages when established in areas where it was not present before (Bonsall 2004). In this sense, regular, long-term monitoring in grasshopper communities of Argentina and China should prove very informative in the long run. Key grasshopper species, in terms of known or potential susceptibility, rarity, and range of geographical distribution, should be designated within areas of pathogen establishment and surroundings. Careful attention should be paid in future surveys to their populations and eventual infection status.

Acknowledgements

I am grateful to Dr. G. Morris and the anonymous reviewers for the suggestions and comments that improved the manuscript. This work was in part possible through a grant (number 2062) from “Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET)”.

References


Table 1. Species of Orthoptera, by continent, family, and subfamily, known to be susceptible to Paranosema locustae. (N) natural infection in a wild host, (I) infection in a wild host after an introduction event of the pathogen, (E) experimental infection resulting from a laboratory bioassay, (S) spontaneous infection in a host rearing facility, (A) infection in a wild host after application in a general area where Paranosema locustae is known to be native.

<table>
<thead>
<tr>
<th>Geographic distribution, family, subfamily, species, and infection type</th>
<th>References</th>
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<td>North America (western USA, southern Canada)</td>
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<tr>
<td>Acrididae</td>
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<tr>
<td>Cyrtacanthacridinae</td>
<td>Henry 1969</td>
</tr>
<tr>
<td>Schistocerca americana (E), S. nitiens (= vega) (E)</td>
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<tr>
<td>Gomphocerinae</td>
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<tr>
<td>Aeropedellus clavatus (N), Ageneotettix deorum (N), Amphitornus coloradus (A), Aulocara elliottii (N), Aulocara (= Depranopterna) femoratum (A), Bruneria brunnea (N), Chorthippus curtipennis (N), Cordillacris occidentalis (A), Mermiria bivittata (N), Oepia obscura, (N), Philobrotula quadriradiata (N), Pseoba delaetula delicatula (N)</td>
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<td>Melanoplinae</td>
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<td>Brachypterus obesus (N), Hesperotettix viridis viridis (N), Hypochlora alba (E) Melanoplus alpinus (N), M. bivittatus (N), M. borealis borealis (N), M. boweldichi carus (E), M. confusus (N), M. canneatus (N), M. daesoni (N), M. differentialis (N), M. femurrubrum (N), M. foedus foedus (N), M. gladstoni (E), M. infantilis (N), M. keederi luridus (E), M. latinus (A), M. occidentalis (N), M. puchardii (N), M. sanguinipes sanguinipes (N), Oedaleonotus exiguo (N), Phoetaliotes nebrascensis (N)</td>
<td>Henry 1969, Steinhaus 1951, Ewen 1983, Henry &amp; Oma 1974</td>
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<td>Oedipodinae</td>
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<td>Arphia conspersa (N), A. pseudorobinae (E), Camnula pellucida (N), Conoza wulllala (N), Cratypedes neglectus (N), Diastostes carolinus (N), D. sparsata (N), Encoptolopus costalis (E), Hadrotettix trifasciatus (N), Metator nevadensis (N), M. pardalinus (N), Spharagonom equale (A), S. collare (A), Trachyrhachys kiowae (N), Trimerotropis sp. (N), T. fontana (N), T. gracilis (N), T. inconspicua (N), T. latifasciata (= laticinta) (N), T. pallidipennis (N), Xanthippus corallipes (N)</td>
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<td>Brachyptyla magna (N)</td>
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<td>Diponthus argentinus (I), Zoniopoda tarsata (I)</td>
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Asia (Rajasthan and Vidarbha, India; Inner Mongolia, Hainan and Qinghai, China)

**Acrididae**

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**Australia** (laboratory production)

**Acrididae**

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Europe (locust rearing facilities in England)

**Acrididae**

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Africa (Karoo, South Africa)

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