



Review

Biology, ecology, and management of the bulb mites of the genus *Rhizoglyphus* (Acari: Acaridae)

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Abstract. Bulb mites of the genus *Rhizoglyphus* (Claparède) (Acari: Acaridae) have been identified as pests of many crops and ornamentals in storage, in the greenhouse, and in the field. The most important hosts are species in the family Liliaceae (e.g. *Allium* spp.), but bulb mites will often attack other important crops such as potatoes (*Solanum* sp.) and carrots (*Daucus carota*). Despite their economic importance and broad distribution, the systematics of the genus remains in a state of confusion and is in need of a comprehensive revision. In addition, the field biology and ecology of these mites is not well understood, and methods for sampling, monitoring, and loss assessment are limited. Management of bulb mites is complicated by their short generation time, high reproductive potential, broad food niche, interactions with other pests and pathogens, and unique adaptations for dispersal. Historically, control of these acarine pests has relied on the use of synthetic miticides and insecticides, but this option is now limited due to documented resistance and withdrawal of registration of some products. Alternative control strategies, including cultural and biological control, have shown limited success, but need to be further developed and implemented.

Key words: *Rhizoglyphus*, Acaridae, bulb mite, soil pests, management, *Allium*

Introduction

Mites in the family Acaridae are among the most important acarine pests attacking agricultural and stored product systems. Within this family, bulb mites of the genus *Rhizoglyphus* are economically important pests of plants with bulbs, corms, and tubers. The two most common species, *Rhizoglyphus echinopus* and *Rhizoglyphus robini*, are probably cosmopolitan and damage a variety of crops including onions (*Allium cepa*), garlic (*Allium sativum*), other *Allium* species, *Lilium*, *Hyacinthus*, and

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many other vegetables, cereals, and ornamentals in storage, in the greenhouse and in the field. Management of these soil pests is complicated by the lack of appropriate sampling methods for assessing field populations and predicting outbreaks, a lack of integrated management alternatives, and a limited knowledge of their field biology and ecology.

Despite their broad distribution, broad host range, and frequent mention in the acarological literature, a comprehensive review on the status of *Rhizoglyphus* mites as agricultural pests is lacking. This review provides a general overview of the biology and ecology of *Rhizoglyphus* mites, and outlines current and future pest management practices. We focus on those *Rhizoglyphus* species that attack vegetable crops and ornamentals, but concentrate on *R. echinopus* and *R. robini*, the two species that have been studied in the greatest detail. Our goal is to review the most relevant aspects of *Rhizoglyphus* biology, ecology, behavior, and management in order to provide a framework for the development of future research and control strategies.

Systematics and distribution

The systematics of *Rhizoglyphus* remain in a state of confusion. The first species of the genus *Rhizoglyphus* was described by Fumouze and Robin in 1868 under the name *Tyroglyphus echinopus*. In 1869, Claparède proposed the genus *Rhizoglyphus* with the type species *Rhizoglyphus robini*. Subsequently, many species have been described, principally by Berlese (1897, 1921), Oudemans (1910, 1924a, 1924b, 1937), Fain (1988), Nesbitt (1944, 1988, 1993) and Manson (1972, 1977). A total of 65 species and six subspecies have been ascribed to the genus (see Table 1), but as with many other agricultural pests, bulb mites have experienced frequent changes of name and taxonomic status.

The most serious taxonomic problem relates to the identities of the two most common species, *R. robini* and *R. echinopus*. Although fairly detailed by nineteenth century standards, the original descriptions and illustrations of these species do not provide sufficient detail to absolutely distinguish them from all other forms. In his comprehensive revision of the Acaridae of the Soviet Union, Zakhvatkin (1941) synonymized *R. robini* with *R. echinopus*. His stated concept for the species included mites with the internal scapular setae (sci) short or absent. Zakhvatkin placed the species *R. dujardini*, *R. megnini*, and *R. spinitarsus* as synonyms of *R. echinopus*, and transferred *R. agilis* to the genus *Acotyledon*. Hughes (1948) recognized that there were actually two common species in agricultural situations, one with short sci setae, for which she retained Zakhvatkin's concept of *R. echinopus*, and one with longer sci setae, for which she used the name *R. callae* (Oudemans). Zakhvatkin's and Hughes' interpretations of *echinopus* and *robini*

persisted until the two species were separated by Eynndhoven (1960, 1968, 1972). After careful study of these two species, including characters from the male and female reproductive systems as well as idiosomal setal lengths, Eynndhoven argued that the species with shorter sci setae more closely matched the description of *R. robini* rather than that of *R. echinopus*. Eynndhoven synonymized *R. callae* with *R. echinopus* and *R. solani* with *R. robini*. These concepts have been followed by most subsequent taxonomic workers (Manson, 1972; Fain, 1988), but not in the influential book by Hughes (1976).

Despite these and other problems, including poor descriptions and loss of type specimens, there has been no revision of this economically important genus. Manson (1972) provides the only synthetic treatment to date, but his work is limited in scope to the *Rhizoglyphus* fauna of New Zealand and additional material obtained largely from quarantine sources. Manson placed *Rhizoglyphus hyacinthi* as synonym of *R. echinopus*, and *Rhizoglyphus feculae* and *Rhizoglyphus rhizophagus* as synonyms of *R. robini*. In addition, he transferred *Rhizoglyphus elongatus* to the genus *Schweibia*, and *Rhizoglyphus longitarsis* and *Rhizoglyphus oblongus* to the genus *Sancassania* (= *Caloglyphus*). Taking into account all synonyms (see Table 1) as well as those species that do not belong in the genus (e.g. *R. karachiensis*, *R. rotundatus*, and *R. termitum*), there remain 52 names in current use under the genus *Rhizoglyphus*.

Thirteen *Rhizoglyphus* species have been identified as pests of crops or have been described from agricultural settings, usually in close association with crop plants. The two most common species, *R. echinopus* and *R. robini*, have broad distributions and are probably cosmopolitan. *Rhizoglyphus setosus* has been reported from three countries, while *R. singularis* has been reported from two countries, with one record consisting of mites present on imported tubers. The remaining species are known to occur in only one country. However, the prior taxonomic confusion of these and other species prevents use of most published literature to compile accurate estimates of their true distributions.

Inferences about *Rhizoglyphus* origins and the zoogeographical events leading to their present distribution should be made with caution. First, as is the case with other mites in the family Acaridae, *Rhizoglyphus* mites are generally understudied, and are often overlooked by non-specialists. Even though new species are frequently described (e.g. Nesbitt, 1988; Bonilla *et al.*, 1990; Lin and Ding, 1990; Nesbitt, 1993; Bu and Wang, 1995) the *Rhizoglyphus* fauna remains largely unexplored, particularly in tropical regions. Second, dispersal of *Rhizoglyphus* mites due to human activities further complicates our understanding of their biogeography. Bulb mites are often intercepted in commercial shipments of infested crops (e.g. Manson, 1972; Wahdi and Misra, 1973; Nesbitt, 1993), and this mode of dispersal may have contributed significantly to the present distribution, particularly of *R. robini* and *R. echinopus*.

Table 1. List of *Rhizoglyphus* names with references and notes on their taxonomic status.

Species	Reference	Notes
<i>actinidia</i>	Zhang <i>et al.</i> , 1994	
<i>agilis</i>	(Michael, 1903)	= <i>Acotyledon michaeli</i> , Zachvatkin, 1941
<i>algericus</i>	Fain, 1988	
<i>algidus</i>	Berlese, 1921	
<i>alliensis</i>	Nesbitt, 1988	
<i>allii</i>	Bu and Wang, 1995	
<i>balmensis</i>	Fain, 1988	
<i>caladii</i>	Manson, 1972	
<i>callae</i>	Oudemans, 1924a	= <i>R. echinopus</i> , Eynhoven, 1968
<i>caucasicus</i>	(see Zakhvatkin, 1941)	
<i>columbianus</i>	Oudemans, 1924b	
<i>costarricensis</i>	Bonilla <i>et al.</i> , 1990	
<i>crassipes</i>	Haller, 1884	
<i>dujardini</i>	Claparède, 1869	= <i>R. echinopus</i> , Zakhvatkin, 1941, but see text
<i>echinopus</i>	(Fumouze and Robin, 1868)	
<i>echinopus noginae</i>	Voloscuk, 1935	
<i>elongatus</i>	(Banks, 1906)	= <i>Schweibia elongata</i> , Manson, 1972
<i>engeli</i>	Eynhoven, 1968	= <i>R. robini</i> , Fain, 1988
<i>eutarsus</i>	Berlese, 1921	
<i>feculae</i>	Oudemans, 1937	= <i>R. robini</i> , Manson, 1972
<i>frickorum</i>	Nesbitt, 1988	
<i>fumouzi</i>	Nesbitt, 1993	
<i>germanicus</i>	Berlese, 1921	
<i>globosus</i>	Berlese, 1921	= <i>Boletacarus sibiricus</i> , Volgin and Mironov, 1980
<i>grossipes</i>	Berlese, 1921	
<i>howensis</i>	Manson, 1972	
<i>hyacinthi</i>	(Boisduval, 1864) (<i>sensu</i> Banks, 1906)	Probably <i>R. echinopus</i> , Manson, 1972
<i>kangdingensis</i>	Wang, 1983	
<i>karachiensis</i>	Anwarullah and Khan, 1970	Probably <i>Sancassania</i> (B.M. OConnor)
<i>longipes</i>	Berlese, 1921	
<i>longitarsis</i>	Banks, 1906	= <i>Sancassania longitarsus</i> , Manson, 1972
<i>longitarsis californicus</i>	Hall, 1912	
<i>lucasii</i>	(Hughes, 1948)	= <i>R. echinopus</i> (<i>R. callae</i> , Hughes, 1976)
<i>megnini</i>	(Haller, 1880)	= <i>R. echinopus</i> , Zakhvatkin, 1941, but see text
<i>mexicanus mexicanus</i>	Nesbitt, 1949	
<i>mexicanus major</i>	Nesbitt, 1949	
<i>mexicanus minor</i>	Nesbitt, 1949	
<i>minimus</i>	Berlese, 1921	
<i>minor</i>	(see Zakhvatkin, 1941)	
<i>minutus</i>	(Oudemans, 1901)	new combination by Michael, 1903
<i>minutus</i>	Manson, 1972	junior homonym of <i>R. minutus</i> (Oudemans, 1901)
<i>narcisii</i>	Lin and Ding, 1990	
<i>natiformes</i>	Jacot, 1935	
<i>nepos</i>	Berlese, 1921	
<i>nepos nigricapillus</i>	Berlese, 1921	
<i>oblongus</i>	Ewing, 1909	= <i>Sancassania oblongus</i> , Manson, 1972
<i>occidentalis</i>	Sevastianov and Marrosh, 1993	

Table 1. Continued.

Species	Reference	Notes
<i>occurens</i>	Berlese, 1921	
<i>phylloxerae</i>	Riley, 1874	= <i>R. echinopus</i> , sensu Michael, 1903
<i>prasinimaculosus</i>	Ewing, 1909	Immature <i>Rhizoglyphus</i> , Manson, 1972
<i>ranunculi</i>	Manson, 1972	
<i>rhizophagus</i>	Banks, 1906	= <i>R. robini</i> , Manson, 1972
<i>robini</i>	Claparède, 1869	
<i>robustus</i>	Nesbitt, 1988	
<i>robustispinosus</i>	Ewing, 1910	
<i>rotundatus</i>	Nesbitt, 1944	Probably <i>Sancassania</i> (B.M. OConnor)
<i>sagittatae</i>	Faust, 1918	
<i>setosus</i>	Manson, 1972	
<i>singularis</i>	Manson, 1972	
<i>solani</i>	Oudemans, 1924a	= <i>R. robini</i> , Eyndhoven, 1968
<i>solanumi</i>	Irshad and Anwarullah, 1968	
<i>spinitarsus</i>	Canestrini, 1880	= <i>R. echinopus</i> , Zakhvatkin, 1941, but see text
<i>sportilionensis</i>	Lombardini, 1948	
<i>tacitri</i>	Manson, 1972	
<i>tardus</i>	Volgin, 1952	
<i>tarsalis</i>	Banks, 1906	
<i>tarsispinus</i>	Oudemans, 1910	
<i>termitum</i>	Womersley, 1941	Not <i>Rhizoglyphus</i> (B.M. OConnor)
<i>trouessarti</i>	Berlese, 1897	
<i>vicantus</i>	Manson, 1977	
<i>zachvatkini</i>	Volgin, 1952	

Host plants, crop damage, and loss assessment

Host plants and crop damage

Rhizoglyphus mites attack a variety of plants but are most often associated with members of the Liliaceae family. A list of mite species, plants affected, geographical location, and references is provided in Table 2. Among the most important hosts are onions, garlic, rakkyo (*Allium chinense*), Chinese chives (*Allium tuberosum*) and other *Allium* species (see Manson, 1972; Kuwahara, 1988). Other Liliaceae such as *Freesia* spp., hyacinth (*Hyacinthus* spp.), lilies (*Lilium longiflorum*) and gladiolus (*Gladiolus* spp.) are often affected in the field, in the greenhouse or in storage (see Manson, 1972).

Attacks on other crops such as carrots (*Daucus carota*; Manson, 1972) and potatoes (*Solanum tuberosum*; Manson, 1972; Wahdi *et al.*, 1973; Mohanasundaram and Parameswaran, 1991) have also been recorded. Bonilla *et al.* (1990) described *Rhizoglyphus costarricensis* collected from rice (*Oryza sativa*) seeds in Costa Rica, and *R. echinopus* and *R. robini* are often collected from rice straw (e.g. Nakao, 1991). In addition, *R. robini* has been reported as affecting rye (*Secale cereale*; Wasilyk,

Table 2. List of *Rhizoglyphus* mites reported as pests, crops and ornamentals affected, and geographic location.

Species	Crop affected	Country
<i>algericus</i>	<i>Gladiolus</i> sp.	Algeria ¹
<i>alliensis</i>	<i>Allium sativum</i>	Mexico ²
<i>allii</i>	<i>Allium sativum</i>	China ³
<i>caladii</i>	<i>Caladium</i> sp.	New Guinea ⁴
<i>costarricensis</i>	<i>Oryza sativa</i>	Costa Rica ⁵
<i>echinopus</i>	<i>Allium bakeri</i>	Japan ⁶
	<i>Allium cepa</i>	Argentina (as <i>R. callae</i>) ⁷ , India ⁸ , Russia ⁹
	<i>Allium sativum</i>	India ¹⁰ , Korea ¹¹ , New Zealand ⁴ , Romania ¹² , Spain ¹³
	<i>Capsicum</i> sp.	India ¹⁰
	<i>Curcuma domestica</i>	India ¹⁰
	<i>Freesia</i> sp.	UK ¹⁴
	<i>Gladiolus</i>	Argentina (as <i>R. callae</i>) ⁷ , New Zealand ⁴
	<i>Hyacinthus</i> sp.	Argentina (as <i>R. callae</i>) ⁷ , New Zealand ⁴ , Russia ¹⁵
	<i>Iris</i> sp.	New Zealand ⁴
	<i>Lolium longiflorum</i>	USA (as <i>R. hyacinthi</i>) ^{16,17}
	<i>Narcissus</i> sp.	Canada ¹⁸ , New Zealand ⁴ , Russia ¹⁵ , Scotland ¹⁹ , UK ¹⁴
	<i>Solanum</i> sp.	France ²⁰ , India ¹⁰ , USA (as <i>R. phylloxerae</i>) ²¹
	<i>Tulipa</i> sp.	Netherlands ²² , New Zealand ⁴ , Russia ¹⁵
<i>engeli</i>	<i>Freesia</i> sp.	Netherlands ^{23,24}
	<i>Lilium</i> sp.	Netherlands ²⁴
	<i>Gladiolus</i> sp.	Netherlands ²⁴
<i>fumouzi</i>	<i>Narcissus</i> sp.	Canada (from Netherlands) ²⁵
<i>narcissi</i>	<i>Narcissus</i> sp.	China ²⁶
<i>nepos</i>	<i>Hypomoea</i> sp.	Italy ²⁷
<i>robini</i>	<i>Allium cepa</i>	Israel ²⁸ , Japan ²⁹ , Mexico ³⁰ , New Zealand ⁴ , USA ³¹
	<i>Allium chinense</i>	Japan ^{32,33,34}
	<i>Allium fistulosum</i>	Taiwan ³⁵
	<i>Allium porrum</i>	Taiwan ³⁵
	<i>Allium sativum</i>	Egypt ³⁶ , Israel ²⁸ , New Zealand ⁴
	<i>Allium tuberosum</i>	Japan ^{32,33,34}
	<i>Daucus carota</i>	New Zealand ⁴
	<i>Freesia</i> sp.	Japan ^{32,34} , UK ¹⁴
	<i>Gladiolus</i> sp.	China ³⁷ , New Zealand ⁴ , Taiwan ^{35,38} , USA ^{39,40}
	<i>Iris</i> sp.	New Zealand ⁴
	<i>Lolium longiflorum</i>	Japan ^{32,34} , New Zealand ⁴ , USA ^{41,42}
	<i>Narcissus</i> sp.	Canada ¹⁹ , New Zealand ⁴ , UK ¹⁴
	<i>Solanum tuberosum</i>	New Zealand ⁴
	<i>Secale cereale</i>	Poland ⁴³
<i>robustus</i>	<i>Allium sativum</i>	Mexico ²
<i>singularis</i>	<i>Dioscorea</i> sp.	India ¹⁰ , New Zealand (from India) ⁴
<i>setosus</i>	<i>Allium cepa</i>	Taiwan ⁴⁴
	<i>Allium porrum</i>	Taiwan ⁴⁴
	<i>Allium sativum</i>	Taiwan ⁴⁴
	<i>Caladium</i> sp.	New Guinea ⁴
	<i>Lilium</i> sp.	Taiwan ⁴⁴
	<i>Gladiolus</i> sp.	Taiwan ⁴⁴
<i>solanumi</i>	<i>Solanum</i> sp.	Pakistan ⁴⁵
<i>tacitri</i>	<i>Citrus</i> sp.	Tahiti ⁴
<i>tardus</i>	<i>Allium cepa</i>	USSR ⁴⁶
<i>tarsalis</i>	<i>Sugar Beets</i>	USA ⁴⁷

1976) and wheat (*Triticum* sp.; Gerson *et al.*, 1983). In New York, USA onion fields, *R. robini* infests rye, barley (*Hordeum vulgare*), and oats (*Avena sativa*) plants used as cover crops and windbreaks, a factor that may contribute to their persistence and outbreaks (Díaz, 1998).

Bulb mites attack the roots and other subterranean structures of plants, but are also occasionally collected on the leaves and stems of infested Liliaceae (e.g. Latta, 1939). Seeds of a variety of crops are also affected. For example, *R. costarricensis* attacks the seeds of *O. sativa*, and mites are often found protected inside the seed coat (Bonilla *et al.*, 1990). Similar behavior has been observed on *R. robini* attacking barley, oats and rye in New York (Díaz, 1998). Infestations of corms and bulbs are characterized by penetration through the basal plate or outer skin layer and subsequent establishment in the inner layers (Latta, 1939; Okabe and Amano, 1991). Condition of bulbs and corms may affect rates of colonization and establishment. For example, Okabe and Amano (1991) showed that colonization of rakkyo bulbs by *R. robini* occurs faster in bulbs infested with *Fusarium* than in healthy ones. Also, mite populations grew faster on *Fusarium*-infested bulbs, suggesting that infestation by this pathogen creates conditions favorable to mite development. Alcohols isolated from *Fusarium*-infested bulbs increase the attractiveness of damaged bulbs to mites (Shinkaji *et al.*, 1988b; Okabe and Amano, 1990). The increased attractancy and rates of colonization and population growth associated with bulb damage can potentially impact mite management practices. In New York, for example, damaged

◆ Footnotes to Table 2

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|--|---|
| ¹ Fain 1988 | ²⁵ Nesbitt 1993 |
| ² Nesbitt 1988 | ²⁶ Lin and Ding 1990 |
| ³ Bu and Wang 1995 | ²⁷ Berlese 1921 |
| ⁴ Manson 1972 | ²⁸ Gerson <i>et al.</i> 1985 |
| ⁵ Bonilla <i>et al.</i> 1990 | ²⁹ Nakao 1991 |
| ⁶ Tomonaga 1963 | ³⁰ Estebanes-Gonzalez and Rodriguez-Navarro 1991 |
| ⁷ Mauri 1982 | ³¹ Rawlins 1955 |
| ⁸ Wadhi <i>et al.</i> 1971 | ³² Kuwahara 1986 |
| ⁹ Lazurina 1976 | ³³ Shinkaji <i>et al.</i> 1986 |
| ¹⁰ Mohanasundaram and Parameswaran 1991 | ³⁴ Kuwahara 1988 |
| ¹¹ Choi <i>et al.</i> 1988 | ³⁵ Chen and Lo 1987 |
| ¹² Cindea 1982 | ³⁶ Kassab and Hafez 1990 |
| ¹³ Del Estal <i>et al.</i> 1985 | ³⁷ Wang 1983 |
| ¹⁴ Wilkin <i>et al.</i> 1976 | ³⁸ Wang and Lin 1986 |
| ¹⁵ Kuznetsov and Tkachuck 1972 | ³⁹ Poe 1971 |
| ¹⁶ Garman 1937 | ⁴⁰ Noble and Poe 1978 |
| ¹⁷ Latta 1939 | ⁴¹ Ascerno <i>et al.</i> 1981 |
| ¹⁸ Andison 1951 | ⁴² Lindquist and Powell 1976 |
| ¹⁹ Gray <i>et al.</i> 1975 | ⁴³ Wasylik 1976 |
| ²⁰ Bedin 1982 | ⁴⁴ Ho and Chen 1987 |
| ²¹ Banks 1906 | ⁴⁵ Irshad and Anwarullah 1968 |
| ²² Munk 1972 | ⁴⁶ Volgin 1952 |
| ²³ Brouwer 1974 | ⁴⁷ Banks 1906 |
| ²⁴ Muller 1976 | |

and cull onions are often colonized by bulb mites (Díaz, 1998), a factor that may contribute to mite outbreaks during the following growing season.

Interactions between bulb mites and fungi and bacteria have received considerable attention in the literature. Price (1976) reported passage of viable *Verticillium albo-atrum* propagules through the alimentary canal of *R. echinopus* after the mites fed on colonies, conidia and microsclerotia of the fungus, and suggested the possibility of mite involvement in fungal epidemiology. Baker (1983) observed that viable *Fusarium* and *Cylindrocarpon* propagules could be recovered from the fecal pellets of *R. robini* growing on a substrate of these pathogenic fungi, and suggested that the mite should be considered a vector of these diseases. Ascerno *et al.* (1983) used a combination of fungicides and acaricides to study the dynamics of interactions between *R. robini* and root rot (*Pythium ultimum*) on lily bulbs and concluded that suppression of the pathogen was possible only when mite populations were low. Poe *et al.* (1979) demonstrated acquisition and retention of *Pseudomonas marginata* by *R. robini*. Under laboratory conditions, dissemination of this pathogen occurred for a maximum of three days, which would limit the mite's role as a vector to local situations. Because surface sterilization of mites does not affect transmission (Noble *et al.*, 1978), propagules must be carried within the alimentary tract.

Passage of viable bacterial and fungal propagules through the mite's gut is not sufficient evidence of a vectoring ability by the mite, especially because other mechanisms may be involved. Beute and Benson (1979) have suggested that soil microfauna can contribute to the induction of root diseases by: (1) creating ports of entry for the pathogen; (2) accumulating inoculum at infection sites; and (3) altering disease susceptibility of the host. The extent to which some of these mechanisms may be involved in disease transmission by bulb mites remains to be determined. In addition, vectoring by mites may play only a minor role in the spread of diseases. Gray *et al.* (1975) suggested that vectoring of smoulder (*Sclerotinia narcissicola*) in *Narcissus* by *R. echinopus* may be of little importance because incidence of the disease in commercial stocks is already high. Effects of vectoring may also be negligible in soils possessing a high inoculum of pathogens (e.g. some muck soils, Abawi and Lorbeer, 1971).

Loss assessment and sampling

Assessment of crop losses due to pest damage is necessary for the development and testing of pest control strategies. In addition, loss assessment is used by farmers choosing among alternative control strategies, and economic damage thresholds (see Stern *et al.*, 1959; Gutierrez, 1987) are often used when making decisions about implementation of these strategies. Despite this, little data are available on loss assessment due to *Rhizoglyphus* spp. infestations. Rawlins (1955) stated that yield from onions infested with *R. robini* was reduced sharply in infested areas, but provided no quantitative estimates of losses. Other authors have provided better

estimates of the potential of this pest for reducing crop yields. For example, Poe (1971) reported that infestation rates by *R. robini* were greater than 50% on *Gladiolus* corms planted in sand in Florida, USA. Wang (1983) observed losses that ranged between 54.2% to 90% on *Gladiolus* infected with *R. robini* in China. The number of infested corms varied with plant developmental stage and season. More recently, Nakao (1991) observed 30% damage due to *R. robini* on Welsh onion (*Allium fistulosum*) seedlings grown in the greenhouse. An average of 13 mites per infested plant and 10 mites per 100 g of soil were observed.

Few researchers have used an experimental approach to damage loss assessment. Jefferson *et al.* (1956) showed that fumigation with metam sodium decreased the incidence of bulb mites and diseases in *Gladiolus* sp., and resulted in corm yield increases that ranged from 280% to 1,100% when compared to untreated bulbs. However, effects of bulb mite reduction could not be separated from effects of reduction on disease incidence. Ascerno *et al.* (1981) used a combination of acaricides and fungicides to study the combined effects of root rot and *R. robini* on greenhouse-grown lilies. Significantly more mites were recovered from control (97.8 mites/pot) and mite-inoculated (369.2 mites/pot) corms than from acaricide-treated corms (5.9 mites/pot). However, quality of corms improved only under combined acaricide and fungicide treatments. Further examination of this system (Ascerno *et al.*, 1983) showed that significant mite-pathogen interactions played a role in the establishment of both pests. This may be a confounding factor when making loss assessment due to bulb mite damage, especially because it may be difficult to determine which organism is the primary invader.

Efficient sampling and monitoring of bulb mite populations is necessary to determine pest distribution and to assess the impact of control measures effectively. Unfortunately, established quantitative approaches for assessing field populations of bulb mites are scarce. Traditionally, assessment consists of manual inspection of infested plants or stored products (e.g. Latta, 1939; Rawlins, 1955). Reliance on this method, particularly in the field, may be inadequate because visible signs of damage may not be apparent until mite outbreaks are well advanced. Gerson *et al.* (1985) utilized garlic-baited traps to sample and monitor *R. robini* populations in garlic and onion fields in Israel. Traps were an effective sampling tool and provided information on mite phenology and abundance from fields under varying conditions. In New York, garlic-baited traps have been useful to detect the presence of *R. robini* and give estimates of their abundance in muck soils (Díaz, 1998). Mite abundance in four fields planted with onions was low early in the growing season (early to mid spring), increased during the summer, and then declined as the harvest approached in late summer. However, in two other fields mite populations declined by mid-summer. These results are consistent with those of Gerson *et al.* (1985), who found that mite populations in fields planted with wheat were lower during the summer than during the fall and spring. As they suggest, increased temperatures and dry soil may account for the observed patterns of abundance.

Biology and ecology

Knowledge of the biology and ecology of *Rhizoglyphus* mites under field conditions remains limited. However, there have been significant advances in our understanding of many aspects of the basic biology of these pests during the last twenty years.

Reproduction and life cycle

The developmental stages in the *Rhizoglyphus* life cycle are: egg, larva, protonymph, heteromorphic deutonymph, tritonymph, and adult. We follow Houck and OConnor (1991) and use the term heteromorphic deutonymph instead of hypopus to refer to this specialized, facultative stage (see below). The life cycle and environmental factors affecting development, longevity, and reproductive potential of *Rhizoglyphus* are presented in Figure 1.

Reproduction in *Rhizoglyphus* appears to be strictly sexual (e.g. Woodring, 1969; Gerson *et al.*, 1983). Observations of *R. echinopus* (Garman, 1937) and *R. robini* (Gerson *et al.*, 1983) show that mating begins one to two days after the adults eclose, usually after some feeding has occurred. In *R. robini*, both males and females may copulate several times a day, and copulation may last from 20 minutes up to several

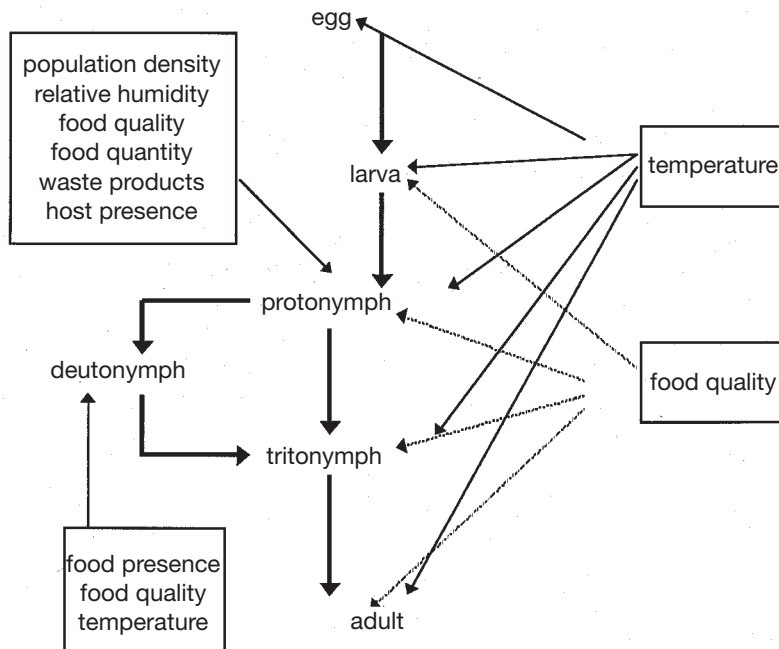


Figure 1. Life cycle and environmental factors affecting the development, longevity, and reproductive potential of *Rhizoglyphus* mites.

hours (Gerson *et al.*, 1983, Radwan and Siva-Jothy, 1996). Duration of mounting increases with increasing male–female ratios (Radwan and Siva-Jothy, 1996). Prolonged copulation (see Alcock, 1994) prevents females from re-mating and thus reduces the risk of paternity loss (Radwan and Siva-Jothy, 1996; Radwan, 1997). Other factors may affect the mating behavior of bulb mites. For example, Gerson and Thorens (1982) showed that food quality strongly affected the frequency of mating in *R. robini*. Mites grown on a peanut diet mated more frequently than mites grown on other diets.

Male polymorphism occurs in some species of the family Acaridae (Hughes, 1976; Woodring, 1969), and Radwan (1993) has suggested that in *Sancassania berlesei* the occurrence of a fighter morph may be adaptive because fighter males in small populations may kill all the males and monopolize the females. Two male morphs have been identified in *R. robini*: a fighter male with a modified third pair of legs, and a nonfighter male with unmodified legs, but the role of fighter males on reproduction in this species, as well as the mechanisms underlying formation of heteromorphic males are not fully understood (Radwan, 1995).

Fertilization in *Rhizoglyphus* is internal. Females store sperm in the *receptaculum seminalis*, and eggs are fertilized before passing through the oviduct and finally the ovipore (Baker and Krantz, 1985). Gravid females can carry a variable number of eggs (Woodring, 1969) which are laid one at a time and in a random fashion (Garman, 1937; Woodring, 1969). The number of eggs laid by individual females can be quite variable, and oviposition is affected by many factors, including temperature and food quality. Sekiya (1948) reported that *R. echinopus* females grown on *A. bakeri* laid 460 eggs per female at 24 °C and 436 eggs per female at 27 °C. Woodring (1969) reported an average of 285 eggs per female for the same species grown on mealworms *Tenebrio molitor*, at 22–24 °C, and Kuznetsov and Tkatchuk (1972) reported an even lower value (109 eggs per female) when the species was grown on *Gladiolus* corms at 18–25 °C.

Oviposition rates appear to be higher in *R. robini* than in *R. echinopus*, but effects of food quality are also observed. For example, Gerson *et al.* (1983) examined the oviposition rates of *R. robini* grown on different diets and temperatures, and reported that at 27 °C females grown on peanuts laid 693 eggs per female over 40 days while those grown on garlic laid an average of 400 eggs per female over 31 days. For this species, Fashing and Hefele (1991) observed a rate of 661 eggs per female over 25.6 days when grown on Bot and Meyer (1967) medium at 27 °C. Temperature also has a marked effect on *R. robini* oviposition rates. For example, Gerson *et al.* (1983) observed that at 16 °C females grown on garlic laid an average of 133 eggs, while at 35 °C no eggs were produced. Both values were significantly lower than those observed for mites grown on the same diet at 27 °C (see above). However, Raut and Sarkar (1991) reported that while a gradual increase in temperature may result in higher oviposition rates, the highest rates were observed when mites were kept at a

variable room temperature (14–34 °C), suggesting that temperature fluctuations may be favorable for maintaining the different metabolic activities of the mite.

Duration of the ontogenic stages is affected by both temperature and relative humidity. For example, Garman (1937) observed that in a *Rhizoglyphus* mite (possibly *R. echinopus*) hatching occurred in 6.5–7 days at 16–21 °C, and 3–4 days at 21–27 °C. Woodring's (1969) observations on *R. echinopus* (5 days at 23 °C) are consistent with these data. Gerson *et al.* (1983; see Table 3) showed that in *R. robini* hatching is faster at higher (≥ 27 °C) rather than lower (< 27 °C) temperatures. However, Fashing and Hefele (1991) showed that hatching took longer at 35 °C than at 27 °C.

Development of subsequent immature stages is also faster at higher rather than lower temperatures. For example, development of *R. robini* larvae, proto-, and deutonymphs grown on the same diet is faster at 27 °C than above or below that temperature (Gerson *et al.*, 1983; Fashing and Hefele, 1991; Raut and Sarkar, 1991). Transformation rates of deutonymphs are also affected by temperature. Baker (1983) showed that while high temperatures favored transformation of *R. robini* deutonymphs, relative humidity had no effect on transformation rates of mites reared on Bot and Meyer media. At 15 °C only 24% of the deutonymphs molted, with a mean duration of 12.2 days. The highest percentage of deutonymphs (87%) molted at 31 °C, with a mean duration of 2.5 days. Relative humidities in the range of 40–95% had no effect on molting when the mites were held at 26 °C. In contrast, Capua and Gerson (1983) showed that in this species (reared on peanuts) transformation rates were higher at 16 °C (88.3%) and 24 °C (93.2%) than at 27 °C (67%) or 35 °C (51.6%). Molting did not occur at relative humidities below 93%, and more transformations occurred when relative humidity was held at 100%.

Effects of food quality on development of immature *R. robini* have been documented (see Table 3). At a constant temperature (27 °C), development of larvae, proto-, and tritonymphs is faster for mites grown on a peanut diet than on a garlic diet or a diet consisting of filter paper (Gerson *et al.*, 1983). Similarly, Baker (1983) showed that deutonymph transformation rates were higher (over 80%) for mites grown on a plant substrate than for mites grown on an animal substrate (below 62%). However, Rhoades *et al.* (1989) showed that in this species transformation rates were generally high, and that they did not differ significantly between bulb mites grown on several species of plant pathogenic fungi and an agar control.

Variation in the duration of each developmental stage and differences in transformation rates may be the result of the interplay between several environmental variables such as temperature (see Sibly and Atkinson, 1994) and diet (Stearns, 1992). However, other factors, such as geographical trends in developmental time (see Nylin and Gotthard, 1998), must be taken into consideration when developmental data is evaluated.

The life cycle is completed with the appearance of adults. Observed sex ratios are 1:1 for *R. echinopus* (Woodring, 1969) and *R. robini* (Gerson *et al.*, 1983). Longevity of both sexes is affected by temperature and food quality. Gerson *et al.* (1983)

Table 3. Duration of development (in days) for *Rhizoglyphus robini* grown on different diets and at different temperatures. Duration shown as a range when such data was available.

Stage	Garlic ^a				Peanuts ^a	Filter paper ^a	Bot and Meyer ^b			Potato ^c				
	16 °C	22 °C	27 °C	35 °C	27 °C	27 °C	16 °C	27 °C	35 °C	15 °C	20 °C	25 °C	30 °C	14–34 °C
Egg	10.7	5.7	3.6	3.4	3.3	3.5	7–13	3–5	4–9	11–13	5–7	3–5	2–5	3–7
Larva	13	6.5	3.0	3.5	2.6	9.5	5–12	3–7	3–4	–	–	–	–	–
Protonymph	7.3	4.6	2.8	4.2	2.4	15.4	5–8	1–3	2–3	3–7	2–6	2–5	2–4	3–6
Tritonymph	9.2	4.4	2.6	4.1	2.1	10.7	7–16	2–3	2–4	7–10	8–9	7–9	6–9	5–8
Adult	–	–	–	14.3	–	15.1	–	–	–	–	–	–	–	–
Male	–	–	62	–	73	–	–	56–130	–	4–11	5–9	5–7	4–8	4–16
Female	–	–	31	–	40	–	–	32–68	–	6–17	7–13	7–18	6–11	6–27

^a Gerson *et al.* 1983

^b Fashing and Hefele 1991

^c Raut and Sarkar 1991.

showed that when *R. robini* is grown on garlic, longevity of females and males (31 and 62 days respectively) is higher at 27 °C than at 35 °C (14.3 days for both sexes). Mites grown on peanuts at 27 °C lived longer (40 days for females and 73 days for males). Generation times were 56.33 days on garlic at 16 °C, 22.48 days on garlic at 27 °C, and 19.48 days on peanuts at 27 °C. Threshold of development was 11.8 °C, with an average of 184.8 degree days necessary to complete the life cycle. In *R. echinopus* threshold of development was 9.7 °C, and 180 degree days were necessary for development (Kuznetsov and Tkatchuck, 1972).

While bulb mite activity may be lower during the colder months, they do not undergo a true diapause, and all stages can be recovered throughout the year (Gerson *et al.*, 1983). Mites may escape from harmful extremes in temperature and humidity by migrating vertically within the soil profile, a strategy common in soil arthropods (Metz, 1971; MacKay *et al.*, 1987). Vertical migration may reduce the efficacy of control measures because chemical or biological control agents may not reach mites inhabiting the deeper soil layers.

Phoresy

Dispersal in *Rhizoglyphus* is accomplished by means of the non-feeding heteromorphic deutonymphs. This facultative stage has unique morphological characters including a reduced gnathosoma, lack of a mouth and chelicerae, a solid non-functional gut, heavy sclerotization, and presence of a sucker plate used for attachment to a host (see OConnor, 1982). Fain (1977) provides a detailed description of the heteromorphic deutonymph in *R. robini*, and Hammen (1982) describes the morphology and development of *R. echinopus*. The biology, evolutionary ecology, and ecological significance of phoresy in astigmatid mites have been extensively reviewed by OConnor (1982) and Houck and OConnor (1991).

Formation of heteromorphic deutonymphs is facultative, with most individuals molting directly from protonymph to tritonymph. In general, occurrence of this stage in the field and in culture is low, but numbers may increase under certain conditions. Deutonymph formation can be induced by low food quality and quantity, high concentrations of waste products, and extremes in temperature and humidity (Michael, 1903; Hodson, 1928; Garman, 1937; Woodring, 1969; see also OConnor, 1982). Under the above conditions, formation of deutonymphs is favored because it allows escape from an adverse environment into a new suitable one. However, Luxton (1995) observed that the highest density of *R. robini* deutonymphs in beech soils occurred with the peak of food intake and highest population density. This is consistent with Chmielewski (1973) who suggested that in the Astigmata high population densities induce a tendency to migration and the production of deutonymphs. Dispersal of deutonymphs is achieved via phoretic associations with an arthropod host.

Rhizoglyphus deutonymphs have been recovered from a diverse collection of hosts. Scarab beetles such as *Osmoderma eremicola*, *Bothynus gibbosus*, and *Phyllophaga anxia* are often identified as hosts of *Rhizoglyphus* deutonymphs (e.g Norton, 1973; Rogers, 1974; Poprawski and Yule, 1992). Other beetles, such as *Geotrupes stercorosus* (Marakova 1995) and the curculionid *Stenorchetus gravis* (De and Pande, 1988) are also used as hosts. One species, *Rhizoglyphus frickorum*, has been described only from deutonymphs collected on the geotropine beetle *Frickius variolosus* (Nesbitt, 1988). In addition some Diptera, such as *Scatopse pulicari*, *Phorbia*, *Chortophila*, and *Eumerus* (Garman, 1937; Zakhvatkin 1941) and Siphonaptera (Fain and Beaucournu, 1993) have been reported as carriers of *Rhizoglyphus* deutonymphs. Very little is known about attachment behavior and cues used by deutonymphs for identifying potential hosts (Houck and OConnor, 1991). Attachment to one or both sexes of a host may occur. For example, *R. echinopus* responds mostly to males of the scarab *O. eremicola*, and over 1,000 deutonymphs have been recovered from a single specimen of this beetle (Norton, 1973).

Phoretic associations may play a role in determining mite distribution in agricultural systems where more than one arthropod pest is present. For example, Zachvatkin (1941) observed that *R. echinopus* deutonymphs were often collected in association with dipteran pests of some important crops. In New York, USA, the onion maggot, *Delia antiqua*, is the most important arthropod pest of onions (Ellis and Eckenrode, 1979). In laboratory studies, onion flies preferentially oviposited in bulbs colonized by *R. robini*, and survival and establishment of onion maggots was also higher in bulbs colonized by this mite (Díaz, 1998). However, attachment of *R. robini* to onion flies has not been observed (but see Zachvatkin, 1941).

Nutritional biology

Rhizoglyphus mites usually occupy moist, humid habitats, and are often recovered from decaying vegetation, fungi, leaf litter, and soils rich in organic matter. When associated with living plants, mites are usually found on the decaying subterranean portions. Details of the nutritional biology of the genus are best known for *R. robini* and *R. echinopus*. The two species are best described as generalists, capable of surviving on a variety of organic materials including dead and living plants, seeds, dead arthropods, nematodes, fungi, and manure among others (Woodring, 1969; Sturhan and Hampel, 1977; Baker, 1983; Gerson *et al.*, 1983; Bonilla *et al.*, 1990; Luxton, 1995).

Akimov and Schur (1972) examined the ability of *R. echinopus* to digest a variety of protein compounds including keratin, ossein, and collagen. They concluded that this species was unable to digest these compounds but may survive on associated lipids. In contrast, Barabanova (1976) demonstrated increased proteolytic activity in *R. echinopus* fed a meat diet, suggesting that the mite could digest proteins. Bowman (1981) showed that while both *R. echinopus* and *R. robini* exhibited proteolysis

activity, this was low compared to that of other acarid mites. Gerson *et al.* (1983) reported that *R. robini* was able to complete immature development on a diet consisting of filter paper, which may imply the ability to digest cellulase. However, Woody and Fashing (1993) showed that the ability of the mite to survive on this diet was due mainly to their use of the cellulolytic potential of associated fungi. Finally, lysozyme activity has been reported on both species (Childs and Bowman, 1981). Lysozymes are essential for the hydrolysis of the cell walls of Gram positive bacteria and have also been shown to have chitinolytic activity (Muzzarelli, 1979). This finding is consistent with the passage of Gram-negative bacteria (e.g. *Pseudomonas*) and fungal conidia and microsclerotia through the bulb mite gut.

Microbes play an important role in the nutritional biology of many arthropods, and specialized symbiotic associations have evolved repeatedly in many taxa (Fletcher, 1987; Aluja, 1994; Paine *et al.*, 1997; Douglas, 1988; but see Breznak and Brune, 1994). Other arthropods obtain nutritional benefits by selectively grazing on microbes, feeding on microbially-degraded substrates, or utilizing microbes to compensate for their enzymatic deficiencies (Kaplan and Hartenstein, 1978; Stefaniack and Seniczak, 1983; Werner and Dindal, 1987 and references therein). What role microbes play on the nutritional biology of bulb mites is still unknown, but pathogenic and non-pathogenic bacteria and fungi associated with bulb mite damage, as well as their metabolic products, may constitute an important nutrient source for bulb mites.

Chemical ecology

Chemicals mediate a wide range of behaviors in arthropods, and communication with chemicals is important for many arthropod species living in the soil. While studies on the chemical ecology of *Rhizoglyphus* mites are rare, it is known that chemicals mediate a wide range of intra- and inter-specific interactions in bulb mites, influencing food and habitat findings (Shinkaji *et al.*, 1988a,b) and escape and defense from natural enemies (Kuwahara *et al.*, 1988; Howard *et al.*, 1988).

Baker and Krantz (1984) first reported citral as the alarm pheromone in *R. robini*, but subsequent studies by Kuwahara *et al.* (1988) showed that neryl-formate is the principal component of this pheromone while citral and α -acaridial are minor components. Recently, Akiyama *et al.* (1997) also identified neryl-formate as the active compound in the alarm pheromone of *R. setosus* and two other unspecified *Rhizoglyphus* species, showing that the alarm pheromone is not species-specific. Alarm pheromones are secreted by the paired opisthotal glands, and pheromone discharge elicits escape behavior in surrounding mites (Kuwahara *et al.*, 1979, 1980). In addition to alarm pheromones, opisthotal glands secrete a wide variety of compounds, including many hydrocarbons (Howard *et al.*, 1988). While the specific function of these compounds is unknown, these authors have suggested that they play a role in mite defense against predators.

Several workers have suggested additional roles for opisthonthal gland compounds, particularly alarm pheromones. For example, Cole *et al.* (1975) reported that citral possessed antifungal activities and Leal *et al.* (1989) showed that α -acaridial was also a potent fungitoxic compound, confirming the dual role of these alarm pheromone components. In addition, some mite cuticular components have also been shown to possess antifungal activity. Leal *et al.* (1990a) described hexyl rhizoglyphinate isolated from the cuticle of *R. robini*, and showed that the compound inhibited mycelial growth of *Aspergillus niger*, *Fusarium oxysporum*, *Penicillium vermiculatum*, and *Alternaria alternata*. Other cuticular compounds, such as the monoterpenoids robinal (Leal *et al.*, 1990b) and isorobinal (Sakata *et al.*, 1996) have been isolated from this species but their biological activity has not been determined. The role of these novel compounds in bulb mite resistance to acaropathogenic fungi remains to be explored, particularly if fungi are to be incorporated into biological control programs for these mites.

Other mite–fungus interactions are also mediated by chemicals. For example, Noble and Poe (1972) showed that several fungi and bacteria isolated from *Gladiolus* corms attracted bulb mites. Shinkaji *et al.* (1988a) documented the attractancy of *Fusarium* infested rakkyo bulbs to *R. robini*, and showed that the mites were also attracted to culture filtrates of the fungus. Isolation and identification of compounds from *Fusarium* culture filtrates indicates that alcohols (ethanol, n-propanol, isobutanol, iso-pentanol, and 2-methyl-1-butanol) were responsible for mite attraction *in vitro* (Shinkaji *et al.*, 1988b). Okabe and Amano (1990) demonstrated attractancy of these alcohols in sand microcosms, and suggested that combined effects of alcohols and other by-products of *Fusarium* activity may further enhance mite attractancy.

Management

Traditionally, control of bulb mite populations has relied upon the use of synthetic acaricides and insecticides. Increased concerns with the effects of pesticides on non-target species have limited the availability of effective pesticides leading to a decrease in the development of new products for this and other pests (e.g. Casida and Quistad, 1998). In some instances (e.g. onions grown in New York, USA) there are no chemicals available for management of this pest. In spite of this, few efforts have been aimed at developing alternative control strategies for bulb mites.

Chemical control

Early efforts aimed at controlling bulb mite populations in storage and in the field focused on the utilization of fumigants such as methyl bromide, cyanide, carbon disulfide, and metam sodium (Garman, 1937; Rawlins, 1955; Jefferson *et al.*, 1956;

Tanaka and Inoue, 1962; Yathom and Ben-Yephet, 1983). Fumigation proved a valuable strategy, especially for treatment of corms and bulbs in storage and *Allium* crops in the field. While many of these compounds are now unavailable, fumigation with metam sodium is still recommended in certain regions (e.g. California, USA). In addition to fumigants, a wide variety of pesticides have been shown to be effective against bulb mites.

Knowles *et al.* (1988) examined the toxicity of 64 different pesticides to *R. echinopus*, and found that the mite was susceptible to only a few carbamates and organophosphates. Formamidines, pyrethroids, organochlorines, and some specific acaricides were ineffective against this pest at the concentrations tested. Chen and Lo (1989) tested 58 commercially formulated compounds against field collected *R. robini* and *R. setosus*, and obtained similar results. Both mites showed susceptibility to a limited number of carbamates and organophosphates, and were generally tolerant of pyrethroids and specific acaricides. Interpretation of results from *in vitro* studies on pesticide toxicity can be confounded by the difference in sensitivity of different bioassay methods. For example, Chen and Lo (1989) showed that incorporation of pesticides into an artificial diet was more sensitive than spray applications because mortality rates using the same pesticides at the same rates were higher for the artificial diet method. A surface tension method described by Chen (1990) is now considered the most sensitive bioassay for testing toxicity of pesticides to bulb mites (Zhao *et al.*, 1996; Gencsoylu *et al.*, 1998). Mite populations from different localities may differ in their susceptibility to specific pesticides. For example, Shinkaji *et al.* (1986) showed that several populations of *R. robini* collected in Japan differed in their susceptibility to the organophosphates dimethoate and disulfoton.

Differences in susceptibility to specific pesticides among different bulb mite populations are often considered as evidence of resistance (see Uebayashi *et al.*, 1986; Shinkaji *et al.*, 1986; Kuwahara, 1986, 1988). For example, Kuwahara (1988) suggested that decreased susceptibility to dimethoate and disulfoton in local populations of *R. robini* has resulted from continuous use of these pesticides for more than two decades. Cross-resistance to other organophosphates as well as some carbamates has been documented in this species (Kuwahara, 1986; Kuwahara and Hangu, 1988).

Mechanisms of pesticide resistance have been extensively studied in bulb mites, and resistance is known to occur at all pharmacokinetic levels. Reduced cuticular penetration of some pesticides, particularly organophosphates, has been documented in both *R. echinopus* (Hamed and Knowles, 1989) and *R. robini* (Kuwahara *et al.*, 1991), but this mechanism may play only a minimal role in overall resistance levels. Resistance is mainly conferred by increased detoxification of pesticides through several metabolic pathways. For example, enhanced oxidative metabolism is responsible for resistance to many classes of pesticides, and oxidase-mediated detoxification is known to occur in both *R. echinopus* and *R. robini* (Scott and Knowles, 1985; Hamed

and Knowles, 1988; Knowles *et al.*, 1988; Kadir and Knowles, 1989; Capua *et al.*, 1990b). Hydrolases (Capua *et al.*, 1990b; Kuwahara *et al.*, 1991; Cohen *et al.*, 1993) and esterases (Capua *et al.*, 1990a) play a significant role in the metabolism of organophosphates and pyrethroids in *R. robini*. In addition, Glutathione-S-transferase enzymes confer resistance to some organophosphates in *R. robini* (Cohen and Gerson, 1986; Capua *et al.*, 1991). Finally, resistance to pesticides can be achieved by reduced neuronal sensitivity to chemicals. For example, altered cholinestareases, with reduced sensitivity to organophosphates and carbamates, may be potentially involved in resistance to these pesticides in *R. echinopus* (Errampalli and Knowles, 1990, 1991).

Cultural control

Manipulation of the environment in ways that make it unfavorable for the colonization, reproduction, and survival of pests can prove to be an effective strategy for suppression of bulb mite populations. Among these cultural control methods are rotation, improved storage systems, intercropping, mixed cropping, manipulation of sowing dates, and management of weed and field margins (Dent, 1991). Few of these methods have been tested or implemented for bulb mite control.

Garman (1937), Latta (1939), and others tested immersion of bulbs in hot water and treatment of bulbs with water vapor for the control of *R. echinopus* on *Lilium* and *Hyacinthus* bulbs in storage. Mite mortality was generally high, but significant amounts of damage to bulbs resulted from both treatments. While hot water or vapor treatments have no applicability in the field, other techniques, such as solarization, also attempt to use the mite's sensitivity to high temperatures for their control. Solarization involves the use of polyethylene soil mulches to trap solar energy so that heat can act as a lethal agent for pest control (Katan, 1981). Solarization has been effective for controlling *R. robini* populations in the field in Israel (Gerson *et al.*, 1981). Complete mite eradication down to 30 cm was observed after 30 days, and mite populations on treated fields were only half the size of populations on untreated ones one year following treatment.

There are two major concerns with the adoption of solarization for control of soil pests. First, the effectiveness of solarization will depend on soil physical variables such as particle size, compaction, and soil water and organic matter content (see Katan, 1981 and references therein). For example, heat flux in soils is limited by both a low water content and high organic matter (Hillel, 1982). Thus, achieving optimal conditions for solarization may require irrigation and a prolonged treatment, which may often be expensive and not feasible. A second concern is the effect of solarization on non-target species, particularly beneficial arthropods. Zaki (1991) studied the effect of solarization on soil mites in cantaloupe (*Cucumis melo*) and showed that significant reductions in the guild of gamasid predatory mites occurred. Depriving

bulb mites of alternate plant hosts may prove a valuable management strategy. For example, Gerson *et al.* (1985) found that *R. robini* was able to utilize and survive on wheat planted in fields where a previous crop of onions had been severely infested with bulb mites. In New York, USA bulb mites have been found to utilize barley, oats, and rye used as winter cover crops and spring windbreaks in onion fields (Díaz, 1998). Interestingly, laboratory studies showed that bulb mites preferred barley, oats, and rye over onion bulbs and other seed types (Díaz, 1998). Replacing barley, oats, and rye with less palatable plants may result in lower mite populations in mite infested fields.

Biological control

Efforts to develop biological control programs for bulb mites have taken place in a number of countries, and have focused mostly on the use of predatory mites, particularly Mesostigmata. In general, these early efforts have been limited to examination of predator behavior and their ability to feed and reproduce on a bulb mite diet. In Egypt, Zedan (1988) reported that protonymphs, deutonymphs, and adults of *Hypoaspis aculeifer* feed and develop on all stages of *R. echinopus*. Reproductive potential of the predator was highest when it fed on adult prey, but less prey was consumed. Ragusa and Zedan (1988) examined interactions between these two species collected from local populations in Italy, and found that both immature and adult *H. aculeifer* preferred to feed on immature rather than adult *R. echinopus*. In contrast to Zedan (1988), reproductive potential was highest when predators fed on a diet of eggs and immatures of *R. echinopus*. Lesna *et al.* (1995) showed that local populations of *H. aculeifer* often differ in their feeding preference and reproductive potential and suggested that it may be advantageous to exploit these 'local' strains as biological control agents.

Lesna *et al.* (1996) showed that *H. aculeifer* could suppress bulb mite populations on lilies under laboratory conditions and in storage. Suppression of prey was affected by both the spatial scale and the structural complexity of the habitat, with bulb mite populations declining faster in the simpler and the smaller habitats. Further studies are needed to evaluate the role of predatory mites under the more complex field conditions.

A large variety of organisms including viruses, bacteria, protozoans, fungi, and nematodes are known to attack mites (see review by Poinar and Poinar, 1988) and have the potential for being used as biocontrol agents. However, very little attention has been devoted to the use of these organisms for control of bulb mites. Fungi of the genus *Hirsutella* are of particular importance due to their ability to infest a large diversity of mites (Gerson *et al.*, 1979). Recently however, Szejnberg *et al.* (1997) reported a failure of *Hirsutella thompsonii* to infest *R. robini* obtained from laboratory cultures.

Directions for future research

Rhizoglyphus mites are important pests of many crops worldwide, yet despite their importance, the taxonomic status of many species still remains uncertain. An exhaustive taxonomic revision of the genus should be a first step in our efforts to understand and manage these arthropod pests.

Emphasis should also be placed on determining the mite's phenology under field conditions as well as the physical variables that affect mite distribution and abundance throughout their range. Manipulation of soil conditions can be an effective management tactic, particularly during non-cropping periods when the mite may be more susceptible to environmental stresses.

Improvement of current methods and development of new tools for population and damage loss assessment are necessary in order to develop economic thresholds and to enable the selection of appropriate control measures against these pests. While use of synthetic pesticides may continue for the foreseeable future, concerns about mite resistance and deleterious effects of pesticide usage, necessitates the development of alternative control strategies. Thus, current efforts in the areas of cultural and biological control must be expanded. Among these developing strategies, the use of predatory mites seems very promising, particularly for controlling mite populations in storage or in the greenhouse. However, additional work is needed in both the identification of new natural enemies as well as implementation of these control strategies under field conditions. Research should also focus on the evaluation of acaropathogenic fungi as potential control agents.

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