POINT OF VIEW

Eur. J. Entomol. **90**: 3–10, 1993
ISSN 1210–5759

Diapause and cold hardiness of phytoseiid mites (Acarina: Phytoseiidae)

W. Dean MOREWOOD

Department of Biology, University of Victoria,
Victoria, British Columbia, V8W 2Y2 Canada

Ecophysiology, cold hardiness, diapause, overwintering, geographic distribution, Acarina, Phytoseiidae, *Phytoseiulus persimilis*, *Amblyseius cucumeris*

Abstract. Because of their economic importance as biological control agents, the basic biology of phytoseiid mites has been studied extensively. Diapause induction has been investigated in a number of species, with consistent results; however, very few studies have addressed cold hardiness of these mites. Recent studies of cold hardiness and cold storage of *Phytoseiulus persimilis* Athias-Henriot and *Amblyseius cucumeris* (Oudemans) indicate that cold exposure had greater adverse effects on nondiapausing *A. cucumeris*, which normally overwinter in diapause, than on *P. persimilis*, which do not diapause. This might be explained in terms of adaptations for winter survival in their native environments. Phytoseiid mites are easily mass-reared and enter diapause in a facultative manner, and thus may be ideal subjects for investigation of the relationship between cold hardiness and diapause.

INTRODUCTION

Cold hardiness of terrestrial arthropods has received increasing attention in recent decades (Baust et al., 1982; Lee et al., 1986; Lee & Denlinger, 1991). In addition to providing insights into the physiology and ecology of terrestrial arthropods, studies of cold hardiness yield information of value for such applied areas as pest management and cryopreservation of living systems. One aspect of cold hardiness that is of particular interest is its relationship with diapause because cold hardiness and diapause are important adaptations for overwinter survival of terrestrial arthropods that inhabit regions with cold winters. Studies on the relationship between diapause and cold hardiness have demonstrated that either may occur independently of the other but in some cases cold hardiness is a component of the diapause program or is greatly enhanced by diapause (reviewed by Denlinger, 1991). The purpose of the present article was to review the available information on diapause and cold hardiness of phytoseiid mites, including recent comparative studies of *Phytoseiulus persimilis* Athias-Henriot and *Amblyseius cucumeris* (Oudemans), with emphasis on the relationship between cold hardiness, diapause, and geographic distributions.

A BRIEF REVIEW OF PHYTOSEIID BIOLOGY

Life History

Mites belonging to the family Phytoseiidae are generally known as predators of phytophagous mites and are regarded as the most important natural enemies of spider mites (Helle & Sabelis, 1985). For this reason they have been studied extensively during the past few decades with respect to their basic biology and potential application as biological control agents (reviewed in Hoy, 1982 and Helle & Sabelis, 1985). All phytoseiids have five life stages: the egg, a six-legged larva, eight-legged protonymph and deutonymph stages, and the adult (Sabelis, 1985). Development is typically quite rapid, with mean egg-to-egg developmental periods above 20°C being less than two weeks for almost all species studied (reviewed by Tanigoshi, 1982), and successive generations are produced continually as long as conditions remain favourable. In temperate zones, short daylengths and relatively cool temperature induce a reproductive hibernal diapause in adult females after mating, which represent the only life stage that overwinters (Overmeer, 1985). Overwintering phytoseiid mites have been collected mainly from fruit trees, where they are found in bark crevices and under insect scales (Homoptera, Coccidae) (Putman, 1959; Chant, 1959; Knisley & Swift, 1971; Ivancich Gambaro, 1990).

DIAPAUSE

Diapause has been investigated in a number of species, the focus of this research being almost exclusively on factors involved in diapause induction (reviewed by Overmeer, 1985 and Veerman, 1992). These studies have produced many common results. In all species studied, diapause occurs only in adult females after mating and the most conspicuous characteristic of diapause is the failure of mated females to produce eggs (Overmeer, 1985). Diapausing females also tend to be less active than nondiapausing mites, feed rarely (Hoy & Flaherty, 1970; Rock et al., 1971; Wysoki, 1974; Van Houten et al., 1988; Morewood & Gilkeson, 1991), and are much more resistant to starvation when in diapause (Croft, 1971; Ivancich Gambaro, 1990). Some authors (eg. Croft, 1971; Morewood & Gilkeson, 1991) have noted that the body cavity contents of diapausing mites take on a granular appearance that may represent an accumulation of energy reserves in the form of lipids [Morewood, 1989; see International Journal of Acarology 18(3): cover page 4].

The primary cue for diapause induction is photoperiod and phytoseiid mites show a Type I response (cf. Danks, 1987), entering diapause only when exposed to short daylengths. Reported critical photoperiods range from 11.2 h (Hoy, 1975a) to 15.3 h (Croft, 1971) and vary among populations as well as among species. Within a species, critical photoperiods are longer for populations from high latitudes or high elevations (Croft, 1971), a trend that is common among insects (Danks, 1987).

Temperature also has a strong influence on diapause induction. The length of the critical photoperiod may be somewhat different at different temperatures (Hoy, 1975a) and diapause is often prevented completely if temperatures remain above 20°C or so (Sapozhnikova, 1964; Rock et al., 1971; Hoy, 1975a; Morewood & Gilkeson, 1991). Temperature alone, in the form of a thermoperiodic cycle, can induce diapause when mites are reared in constant darkness and this thermoperiodic response corresponds very closely to the photoperiodic response (Van Houten et al., 1987, 1988).

Phytoseiid mites generally diapause only after being exposed to diapause-inducing conditions throughout their juvenile development; however, a few species have been reported to "switch" into diapause when exposed to diapause-inducing conditions as adults after being reared under nondiapause conditions (Putman, 1962; Hoy, 1975b; Swift, 1987; Van Houten, 1989).

Finally, the ability to diapause is not universal in phytoseiid mites; rather, some species and some populations within a species have been shown to lack a diapause response or to overwinter without diapausing (Wysoki & Swirski, 1971a,b; McMurtry et al., 1976; Overmeer, 1985; see below).

COLD HARDINESS

Very few studies have addressed cold hardiness of phytoseiid mites. The first of these (MacPhee, 1963) consisted of collecting overwintering adult females from apple trees in Nova Scotia, Canada, determining their supercooling points, and monitoring their survival over time at various subzero temperatures. Mean supercooling points, temperatures at which freezing of body fluids occurs, ranged from –28.9°C to –31.4°C and mortality approached 100% within several hours at temperatures ranging from –23.3°C to –28.3°C. Later studies by Knisley & Swift (1971) and Wysoki (1974) made cursory comparisons of cold hardiness in diapausing and nondiapausing mites. In both cases diapausing mites survived roughly twice as long as nondiapausing mites at temperatures ranging from –1°C to –9°C; however, even the diapausing mites did not survive more than a few days at these temperatures.

The most comprehensive study to date was conducted by Van der Geest et al. (1991) using *Amblyseius andersoni* (Chant) [= *Amblyseius potentillae* (Garman) (Chant & Yoshida-Shaul, 1990; Messing & Croft, 1991)] as the experimental animal, a species in which diapause induction has been studied extensively (cf. Van Houten, 1990). In their study, Van der Geest et al. (1991) reported cold hardiness in terms of LT_{50} at –5°C, the number of days' exposure resulting in 50% mortality. The LT_{50} value for diapausing mites was more than three times that for nondiapausing mites when neither group had been acclimated to low temperatures. In addition, survival times increased markedly when diapausing mites were acclimated to 4°C before being exposed to –5°C but increased only slightly when nondiapausing mites were acclimated prior to exposure. These results indicate that diapausing mites are inherently more cold hardy and also have a much greater capacity to respond to low temperature acclimation than nondiapausing mites.

A COMPARATIVE STUDY OF *PHYTOSEIULUS PERSIMILIS* AND *AMBLYSEIUS CUCUMERIS*

Both *P. persimilis* and *A. cucumeris* are commercially mass-reared for use as biocontrol agents in Europe and in North America (Steiner & Elliott, 1987). The ability to hold these mites in cold storage would be a valuable addition to mass production systems. In addition, *P. persimilis* is considered to be "subtropical" in origin (Fig. 1, see below) and is thought to be incapable of entering diapause (Overmeer, 1985) whereas *A. cucumeris* is widespread in temperate zones and is known to diapause (Morewood & Gilkeson, 1991). For these reasons, studies were undertaken to compare cold hardiness of these two species and to determine their suitability for cold storage.

Cold hardiness was evaluated in terms of supercooling points (SCPs), freezing tolerance, and susceptibility to chilling injury in the absence of freezing (Morewood, 1992c). All life stages of both species showed a moderate ability to supercool, with mean SCPs ranging from –19.4°C to –27.1°C, and a close relationship between SCPs and acute mortality demonstrated that both species, including *A. cucumeris* in diapause, were not tolerant of freezing. Non-acclimated mites, taken directly from rearing cultures, survived only very short periods of exposure to subzero temperatures above their SCP (less than 90 min at –12.5°C). In preliminary experiments, survival at subzero temperatures was greatly enhanced by prior acclimation to 6°C or 7°C for one week or especially, in the case of *A. cucumeris*, by rearing under diapause-inducing conditions. However, due to logistic constraints, these preliminary experiments were conducted with small numbers of mites and were not comprehensive enough to provide the basis for firm conclusions. Both species survived a very brief exposure to –15°C; however, female *P. persimilis* showed no adverse affects on subsequent fecundity whereas female *A. cucumeris* laid only half the number of eggs laid by a control group. This would suggest that nondiapausing *A. cucumeris* are very susceptible to chilling injury but that *P. persimilis*, which do not diapause, are not.

In cold storage trials, survival was better at 7.5°C than at 2.5°C and was optimized when both food and a source of moisture were provided (Morewood, 1992a,b). Under these conditions 80% of *P. persimilis*, but only 35% of *A. cucumeris*, survived six weeks of cold storage. Furthermore, subsequent longevity and fecundity of *P. persimilis* were comparable to those of a control group taken directly from mass-rearing cultures whereas fecundity of *A. cucumeris* was low and irregular after cold storage.

These results were unexpected, considering the ecological origins of the two species. In studies such as this, it is important to consider whether the laboratory-reared animals adequately represent wild populations. The mites used in this study were mass-reared under optimal conditions for reproduction and development and thus have not been subjected to any selective pressure that would alter their cold hardiness. In the absence of selective pressure, genetic drift may become a factor; however, genetic drift is unlikely to be significant in the extremely large populations maintained in mass cultures. The fact that *A. cucumeris*, which have been mass-reared under nondiapause conditions for several years, have retained a well-defined diapause response suggests that these mites do not easily lose their natural characteristics. Similarly, Van der Geest et al. (1991) compared their laboratory-reared mites (*A. andersoni*) with mites collected from apple orchards and found no evidence for differing levels of cold hardiness between the two strains. In the case of *P. persimilis* and *A. cucumeris*, comparison of the distribution of collection records for each species to climatic data for the appropriate regions suggested a potential explanation for the unexpected results.

ECOLOGICAL IMPLICATIONS

The geographic distribution of *P. persimilis* is suggestive of a Mediterranean origin followed by inadvertent introduction to southern latitudes with the movement of horticultural products (Fig. 1). Such an hypothesis is open to debate; however, the reported distribution of *P. persimilis* is apparently limited almost exclusively to areas that have a "Mediterranean" type of climate (cf. Boucher, 1975). Similarly, despite introductions for biocontrol purposes in many countries around the world, the only place where *P. persimilis* has been reported to have become established following introduction is in southern California (McMurtry et al., 1978), which also has a Mediterranean climate.

Typical Mediterranean localities often have mean monthly temperatures below 10°C in winter and extreme lows between 0°C and –10°C (Boucher, 1975). Similarly, Hamamura et al. (1976) reported survival of *P. persimilis* overwintered on potted strawberry plants in the field at Hiroshima, Japan, where mean weekly temperatures ranged between 0°C and 10°C from January to March and extreme lows approached –5°C. In the same study, adult females survived up to four days at 0°C and two days at –5°C in laboratory tests. Although the numbers of adult females surviving outdoors declined considerably during the course of the experiment, this is not inconsistent with estimates of natural winter mortality of diapausing phytoseiids in temperate zones (Chant, 1959, 1963; Herbert, 1962; Knisley &

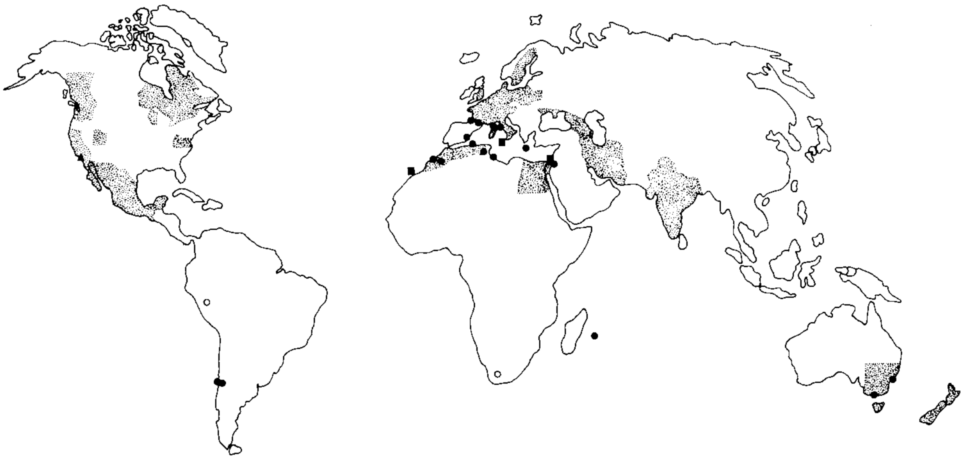

Fig. 1. Geographic distribution of *P. persimilis* and *A. cucumeris*, compiled from de Moraes et al. (1986) with additional records from Womersley (1954), Duso & Liguori (1984), Ridland et al. (1986), Gutierrez & Etienne (1986), Pande et al. (1989), McMurtry & Bounfour (1989), and Allawi (1991). Shaded areas represent nations, states, or provinces from which *A. cucumeris* has been reported; symbols represent collection records for *P. persimilis* (● = collection locality, ○ = exact locality unavailable or uncertain, ▲ = introduced, ■ = both species reported).

Swift, 1971). It appears, then, that *P. persimilis* is capable of surviving substantial periods at moderately cool temperatures and brief exposures to subzero temperatures without subsequent adverse effects on longevity or fecundity, and without the benefit of a diapause.

Published collection records for *A. cucumeris* suggest a broad distribution throughout favourable areas of North America and Europe (Fig. 1), including areas classified as Subarctic (cf. Boucher, 1975). In northern populations, female *A. cucumeris* respond to short daylengths and cool temperatures by entering an imaginal reproductive diapause in preparation to overwinter (Overmeer et al., 1989; Morewood & Gilkeson, 1991); however, this may not be true in other parts of their range. For example, McMurtry et al. (1976) reported that in another widespread species, *A. andersoni*, individuals from the Netherlands (Zeeland, ca. 51.5°N) entered diapause after being reared under short day photoperiods, but individuals from Italy (Fondi, ca. 41°N) did not. In Italy's Po Valley (ca. 45°N), however, male and immature *A. andersoni* disappeared at the beginning of winter and only diapausing adult females survived (Ivancich Gambaro, 1990). Similarly, several phytoseiid species have been reported to remain reproductively active throughout the winter in Israel, with all life stages present on sampled plants, but a few of these overwintered only as adult females at higher elevations (Wysoki & Swirski, 1971a,b). Although diapause may be necessary for overwinter survival in colder temperate areas, the Mediterranean climate is apparently favourable enough to allow some phytoseiid mites to overwinter without diapausing.

Diapausing adult females of *Amblyseius umbraticus* (Chant) (Knisley & Swift, 1971), *Phytoseius finitimus* Ribaga (Wysoki, 1974), and *A. andersoni* (Van der Geest et al., 1991) all survived much longer at subzero temperatures than nondiapausing individuals. This indicates that diapause is a requisite for optimum cold hardiness of the phytoseiid species in which it occurs. Given that diapause prevents development of the ovaries in female phytoseiids (Wysoki, 1974), it is interesting that chilling injury of nondiapausing *A. cucumeris* was expressed as reduced and irregular oviposition. This information implies that, by preventing development of the ovaries, diapause provides protection from adverse effects of low temperature exposure on subsequent fecundity.

Although the results of studies involving cold hardiness and diapause in phytoseiid mites imply a strong link between diapause and cold hardiness, *P. persimilis* has shown a considerable degree of cold hardiness in the absence of any diapause. In fact, *P. persimilis* was more cold hardy than nondiapausing *A. cucumeris* even though the latter species would have to withstand longer periods of time at lower temperatures in order to survive in the northern parts of its range. Expression of such enhanced cold hardiness may be dependent on diapause, considering that only diapausing mites overwinter at high latitudes. The results presented here are consistent with this conclusion but do not provide a firm foundation for it; rather, more comprehensive studies are required to clarify the relationship between diapause and cold hardiness. Phytoseiid mites could prove to be an ideal group for such studies because they are easily mass-reared in the laboratory and readily assessed for diapause status. Furthermore, their diapause is facultative and some species or populations do not diapause at all, allowing for comparison of cold hardiness in nondiapausing and diapausing individuals from the same population as well as comparative studies of diapause and cold hardiness at both interspecific and interpopulation levels.

ACKNOWLEDGEMENTS. Thanks to Olga Kukal, Richard Ring, and Lauritz Sømme for their reviews of the manuscript. Mites for the comparative study were generously provided by Applied Bio-Nomics Ltd., Sidney, British Columbia, Canada. This study was supported by Postgraduate Scholarships from the Natural Sciences and Engineering Research Council (NSERC) of Canada and GREAT (Graduate Research Engineering and Technology) Awards from the Science Council of British Columbia, and by NSERC Operating and Equipment grants to Richard Ring at the University of Victoria.

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Received May 29, 1992; accepted January 20, 1993