

HENK SIEPEL

STRUCTURE AND FUNCTION
OF
SOIL MICROARTHROPOD COMMUNITIES

CENTRALE LANDBOUWCATALOGUS



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Promotor: Dr. L. Brussaard
Hoogleraar in de Bodembiolegie

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OF
SOIL MICROARTHROPOD COMMUNITIES

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WAGENINGEN

behorende bij het proefschrift van Henk Siepel:
Structure and function of soil microarthropod communities

1. Foresie is geen r-geselecteerd kenmerk; het is een manier van vervoer tussen geschikte biotopen die in overigens ongeschikt terrein liggen.
(Dit proefschrift, Binns E.S. 1982, Biol Rev: 57, 571-620)
2. Het gebruik van zich asexueel reproducerende dieren in oecotoxicologische toetsen geeft geen representatieve resultaten voor de soort, laat staan voor groepen van soorten.
(Dit proefschrift)
3. Het actuele gebruik van voedingsmogelijkheden geeft alleen inzicht in de autoecologie van een soort in vergelijking met het potentiële aan voedingsmogelijkheden.
(Dit proefschrift)
4. De mate van chitinaseactiviteit in de populaties van microarthropodesoorten indiceert de mate van ongestoordheid van het afbraakproces van organisch materiaal op zwak zure bodems.
(Dit proefschrift)
5. Bij lage mobiliteit kunnen meer soorten samen voorkomen dan dat er bronnen van bestaan zijn.
(Dit proefschrift, n.a.v. Arthur W. 1987, *The niche in competition and evolution*, Wiley & Sons, Chichester, UK)
6. Uitsluiting door concurrentie is zeldzaam.
(Dit proefschrift, Hardin G. 1960, *Science* 131: 1292-1297)
7. Begrazing van natuurterreinen dient voornamelijk om te laten zien dat het terrein beheerd wordt; de vermeend gunstige effecten op de natuur zijn nooit bewezen.
8. Onderzoek naar dosis-effect relaties in de oecotoxicologie heeft geen betekenis als het niet gekoppeld wordt met autoecologische en systeemoecologische kennis.
9. Oecologen onderschatten de natuurwaarden van het stedelijk en landelijk gebied.
10. Indicatoren voor biodiversiteit zijn een contradictio in terminis.
11. Vergroting van de onvoorspelbaarheid van het milieu bevordert behalve de mobiliteit van de éne groep vooral ook het uitsterven van andere groepen.
12. Onderzoek naar natuurontwikkeling wordt zelden vanaf de bodem opgebouwd.

Voor mijn ouders

Contents

Abstract	7
Voorwoord	9
1. General introduction	11
2. Life-history tactics of soil microarthropods (<i>Biology and Fertility of Soils, in press</i>)	15
3. Applications of microarthropod life-history tactics in nature management and ecotoxicology (<i>Biology and Fertility of soils, in press</i>)	51
4. Feeding guilds of oribatid mites based on their carbohydrase activities (with Elze de Ruiter-Dijkman) (<i>Soil Biology and Biochemistry 25 (1993), 1491-1497</i>)	69
5. Mites of different feeding guilds affect decompo- sition of organic matter (with Frans Maaskamp) (<i>Soil Biology and Biochemistry, in press</i>)	81
6. Coexistence in soil microarthropods (<i>subm.</i>)	95
7. Competitive exclusion is not a general ecological principle (<i>subm.</i>)	117
8. General discussion	121
Summary	131
Samenvatting	133
Curriculum vitae	136

Abstract

Microarthropod species were classified according to life-history tactics and feeding guilds. Twelve life-history tactics were distinguished, based on well-defined life-history traits like the type of reproduction (thelytoky, arrhenotoky, sexual reproduction), oviposition (semelparity, iteroparity), development, synchronization (of the life cycle with environmental conditions), and dispersal (phoresy, anemochory). Examples are given of the distribution of these tactics among microarthropod species occurring in several biotopes, during decomposition of organic matter, and under several types of disturbance and pollution. Thelytokously reproducing species appeared to have higher numbers at sites with a persistent pollution.

Feeding guilds were defined on the basis of gut carbohydrase (cellulase, chitinase, and trehalase) activities. Five species-rich guilds were recognized. In the presence of species able to digest the fungal cell-wall next to cell-contents (called fungivorous and herbo-fungivorous grazers), a higher CO_2 evolution during decomposition of pulverized litter was found than in their absence. In the presence of species able to digest cell-contents only (called fungivorous browsers and opportunistic herbofungivores), in such experiments a lower CO_2 evolution was found than in their absence.

In a simulation model it was tested whether relatively inefficient use of food may be compensated by life-history traits or abilities by which short-term environmental extremes can be overcome. Having the possibility to bridge a relatively long period of food shortage, or withstanding extremes in drought, frost or heat, or having a higher mobility, was indeed shown to result in a better survival of species that use their food relatively inefficiently. This results in the effect that species with different life-history tactics can coexist on the same food sources. Contradictory to the principle of competitive exclusion, species with identical niches may coexist when the mobility of these species is not unlimited.

Key-words: Acari, Collembola, Life-history, Feeding guild, Coexistence, Decomposition, Nature management, Ecotoxicology.

Voorwoord

Hoewel ik al heel jong belangstelling had voor biologie en van alles liep te bekijken als mijn vader en opa aan het vissen waren, had ik nooit gedacht dat ik me met mijten en springstaarten bezig zou houden. Voor ik in oktober 1984 op het toenmalige Rijksinstituut voor Natuurbeheer kwam, wist ik net dat mijten acht poten hebben (met uitzondering van de larfjes) en springstaartjes zes. In het onderzoek op graslanden naar indicatorsoorten en evaluatiemethoden, waar ik me op moest gaan richten, waren dit ook al geen voor de hand liggende groepen. Bij mijn aanstelling werd ik echter geconfronteerd met enige nog uit te werken datasets van deze microarthropoden. Deze datasets waren toch verzameld in het kader van het monitoringonderzoek op graslanden omdat ze volgens Chris van de Bund heel precies de toestand van het grasland aangaven. Chris bracht dit zo overtuigend en stimulerend dat ik niet alleen de datasets uitwerkte en een bemonstering van microarthropoden in het graslandenonderzoek opnam, maar uiteindelijk zelf ook naar de mijten en springstaarten ging kijken. In de loop van het onderzoek bleken inderdaad heel goede indicatoren te vinden onder de microarthropoden, maar dat gold ook voor de grotere insecten en spinnen, die voor een praktijktoepassing de voorkeur kregen.

Maar de teerling was geworpen en ik was geïntrigeerd geraakt door de wereld onder het bodemoppervlak. De talrijkheid van de beestjes, hun soortenrijkdom, hun veelheid aan vormen, ook in ecologisch opzicht, maakten dat ik me nog gauw door Chris liet inwijden in de herkenning van microarthropoden voor Chris in 1987 de dienst verliet en ik formeel op zijn plaats kwam. Overigens bleef Chris ook daarna bereid de determinatie van soorten die ik voor het eerst zag te verifiëren en geen idee was te wild om er eens serieus over door te bomen. Ook de anderen die als klankbord hebben gediend binnen en buiten het maandelijks entomologenoverleg op het instituut wil ik bedanken voor hun opbouwend commentaar, hun suggesties en het kritisch doorlezen van de concepten, met name Frits Bink, Walter van Wingerden, Mari Verstegen, Rob Hengeveld, en bij het modelwerk Hilko van der Voet en Rienk-Jan Bijlsma. Enkele belangrijke hoofdstukken van dit proefschrift waren er misschien nooit gekomen zonder de hulp en inzet van Elze de Rooter en Frans Maaskamp. Ruut Wegman wil ik graag bedanken voor het tekenen van de figuren. Prof. dr. Lijbert Brussaard wil ik bedanken dat hij als promotor op wil treden en voor zijn inspirerend enthousiasme waarmee hij de concepten te lijf ging en van kritisch commentaar voorzag, zodat ze ook voor niet direct betrokkenen leesbaar werden. Furthermore I like to thank Prof. dr. M.B. Usher, who strengthened me in my view that identifications in soil microarthropods should go to the species level as he stated in the

Voorwoord

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Arnhem, 11 juli 1994

Hank Sierp

1

General introduction

The soil fauna is very rich in species; protozoans, nematodes, arthropods and annelids are the major groups of animals, both in number of species, and in biomass. This thesis will focus on the soil arthropods, particularly the microarthropods, the group most rich in species. All soil mites (Acari), and primary wingless insects, predominantly springtails (Collembola) are included in the soil microarthropods. Mites are a subclass of the spiders, which in The Netherlands contains six orders: Metastigmata (ticks), Oribatida (moss mites), Acaridida, Mesostigmata (predatory mites), Actinedida (spider mites, harvest mites, water mites, etc.) and Tarsonemida (with the Actinedida also called Prostigmata). Next to these commonly accepted names many synonyms are used (Van der Hammen 1972). Oribatid mites are the most abundant in forest soils, followed by Collembola and Mesostigmata. Actinedida and Tarsonemida are sometimes very abundant in grassland and arable soils. Acaridida form most of the time a minority in numbers in the soil fauna. With respect to species richness in the soil the Actinedida are the first in rank, but many species live in the vegetation and are found in soil samples only accidentally. Oribatida are next in rank in species richness, followed by Mesostigmata, Collembola, Tarsonemida, and Acaridida.

Species richness is thought to be related to surface: the larger a site the more species can be present (MacArthur & Wilson 1967). The highest species richness among oribatids varies from on average 33 oribatid mite species per 500 cm² (range 23-45) in Central European forests (Moritz 1965) to 45 oribatid species per 250 cm² (range 37-52) in unmanaged Dutch grasslands (Siepel & Van de Bund 1988). Karppinen (1958) found an average of 19 oribatid mite species (range 8-26) per 5 cm² in Finnish forests. Species richness for all microarthropods together is even much higher, up to 108 species per 500 cm² (Siepel & Van de Bund 1988). Assuming that every species has an unique niche, according to the hypervolume model (Hutchinson

1957), and that competitive exclusion leads to minimizing niche overlap (Hardin 1960), one must conclude that in the soil a tremendous variation in resources has to exist (Anderson 1975). Theoretically this may be possible, but are the animal species able to distinguish and select those resources? The alternative solution is that different species may use the same resources (food, shelter, etc.) without mutual exclusion. A less efficient use of resources might be compensated by certain adaptations in the life-history.

The objective of this thesis is to investigate whether a limited number of resources allows the coexistence of a higher number of species. This question requires operational knowledge about the structure and function of soil microarthropod communities. The structure is explained from differences in life-history tactics resulting in different abilities to overcome sudden harsh environmental conditions. The function is explained from different feeding guilds of microarthropods. These guilds are defined on the basis of activities of carbohydrase gut enzymes. The different effects representatives of these feeding guilds have on the rate of decomposition of organic matter may be explained from differences in digestion capacities.

In chapter 2 the life-history traits of soil microarthropods are dealt with to present a solid base for the definition of life-history tactics. Several life-history traits pass in review and the ecological significance of thelytoky, either automictic or apomictic, arrhenotoky, amphitoky, and sexual reproduction are explained. A classification of twelve life-history tactics, based on well-defined, underived traits is presented and compared with the classifications of MacArthur and Wilson (1967), Grime (1977) and Southwood (1977) and with the multidimensional classification of Stearns (1976). For every tactic the functional relation with the most important biotopes is described. Examples of species from each systematic order are given when available.

In chapter 3 a key is presented as a tool for the identification of life-history tactics. Examples of the distributions of microarthropod species among life-history tactics are presented for the soil fauna of a forest, a grassland, and a saltmarsh. The practical applicability of the defined life-history tactics is subsequently illustrated in nature management and ecotoxicology. The common use of asexually reproducing species in ecotoxicology is discussed.

In chapter 4 forty-nine oribatid mites and one acaridid mite are classified in feeding guilds based on their gut carbohydrase activities. Three carbohydrases were selected to differentiate between food sources. Cellulase activity indicates digestion of plant material, including algae, trehalase activity indicates digestion of the cell-contents of fungi,

lichens, and blue-green algae, and chitinase activity indicates that also the fungal cell-walls can be digested. Herbivorous grazers, herbivorous browsers, fungivorous grazers, fungivorous browsers, herbofungivorous grazers, opportunistic herbo-fungivores, and omnivores are proposed as feeding guilds, with grazers able to digest most of the ingested food components, and browsers able to digest the cell-contents only.

In chapter 5 the decomposition of litter by fungi in the presence and the absence of representatives of the five major feeding guilds is studied. The implications of the new classification of feeding guilds for insight into the role of mites in the decomposition of organic matter are discussed.

Differences in efficiency of food-processing may result in a selective advantage of the more efficient mites. In chapter 6 a simulation model is presented to evaluate possible ways of compensation for the less efficient mites by differences in life-history tactics, mobility, or tolerance for short-term extreme conditions (drought, frost, heat, food shortage).

Chapter 7 deals with a special application of the simulation model: the test of the 'principle of competitive exclusion' (Hardin 1960). In the simulation model two species are defined as identical. In a first set of runs both species have no restrictions in mobility (as in a Lotka-Volterra model) and in a second set of runs both species are restricted in their mobility (as usually in nature). The possible co-occurrence of 'identical species' is discussed and related to speciation rates.

In the general discussion (chapter 8) the approach followed in this thesis and the results obtained are evaluated. The traits a species can use to survive, either life-history traits, digestion capacities, or possibilities to overcome short-term extreme conditions, determine the potential range of biotopes that species can inhabit. This may be a better starting point for the coexistence of species understanding in soil than comparisons of species communities and microhabitat characteristics.

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Life-history tactics of soil microarthropods

SUMMARY. In order to provide a sound basis for defining life-history tactics, several life-history traits are reviewed. The ecological implication is explained of thelytoky (automictic or apomictic), arrhenotoky, amphitoky, sexual reproduction, and semelparity, iteroparity, seasonal iteroparity and the relationship between semelparity and juvenile development. Several forms of synchronization of life-cycles with environmental conditions are classified, ranging from the ability to overcome harsh periods during the season to obligate diapause dormancy. Ecologically, this involves adaptations to environmental conditions ranging from irregularly occurring and unpredictable to regularly occurring and predictable. Dispersal traits are grouped in directional migration (phoresy) and undirectional migration (anemochory). A distinction is made between facultative and obligate phoresy and between carrier-specific and carrier-unspecific phoresy. A multi-dimensional system of tactics is presented, based on well-defined underived traits. This system is compared to one- and two-dimensional schemes of MacArthur & Wilson (1967), Grime (1977), and Southwood (1977) and to the multi-dimensional system of Stearns (1976). For every tactic, relationships with the main biotopes where it occurs among species, are given. Examples of species showing certain tactics are given per taxonomic order of microarthropods. The generality of the traits for various groups of organisms and of the classification of life-history tactics developed is discussed.

INTRODUCTION

Many papers have been published on life-history strategies of species during the past few decades. Classifications of life-history strategies are useful in analysing the effect of nature management and of the pollution of biotopes (Grime *et al.* 1988), because species and species groups can be compared. However, there are still very few papers on the life-history strategies within a group of species sharing common traits.

The theory of r- and K-selection of MacArthur and Wilson (1967) is mainly based on differences among species in reproductive traits, in particular the number of eggs laid and the juvenile survival in relation to the stability of the environment. In the classification of life histories, species were placed along a gradient running from r-selected to K-selected species. However, many species may be found in the middle of the gradient. Grime (1977, 1979) found that plants have certain 'K-selected' traits under harsh environments, different from the environments typical of K-selection *sensu* MacArthur and Wilson (1967). Consequently, Grime added stress selection (or adversity selection as it was named later by Greenslade (1983)), defining the plants with K-selected traits in a harsh non-K environment as S-selected. This resulted in a triangle of R-, C-, and S-selection, where R-selection corresponds with MacArthur & Wilson's r-selection and C-selection with their K-selection.

Southwood (1977) drew attention to the role of the habitat as the templet for ecological strategies. In Stearns' (1976) classification of life-history tactics the templet becomes multidimensional.

In this paper a classification of life-history tactics is developed for mites, while Collembola are used to evaluate the suitability of the classification for a taxonomically unrelated group. The main components of the life history of microarthropods are: 1. reproduction (sexual reproduction, thelytokous parthenogenetic reproduction, arrhenotokous parthenogenetic reproduction, semelparity and iteroparity), 2. development (developmental stages and factors that control development), 3. synchronization (diapause, aestivation, and quiescence), and 4. dispersal (mobility, phoresy and anemochory). Patterns in these traits are described as a set that constitutes a tactic *sensu* Stearns (1976) "a set of coadapted traits designed, by natural selection, to solve particular ecological problems. A complex adaptation." Special attention is paid to the relationships between life-history traits and it is discussed whether these are also relevant to other organisms. The classification of life-history tactics defined here will be compared to those of MacArthur & Wilson (1967), Grime (1977, 1979), Southwood (1977, 1988) and Stearns (1976).

REPRODUCTION

Ways of reproduction will be emphasized as life-history traits, rather than the number of eggs produced or the initial rate of population increase which play a central role in the theory of r- and K- selection (MacArthur & Wilson 1967). Although egg production is an important trait, the variation among microarthropods in other reproduction traits is quite high, and,

thereby, suitable for classifying tactics.

Sexual and asexual reproduction

Reproduction in microarthropods is either sexual or parthenogenetic. Parthenogenesis can have several ecologically and genetically different forms: 1) arrhenotoky: unfertilized eggs hatch into males (haploid) and fertilized eggs become females; 2) thelytoky: asexual reproduction of females giving female offspring, resulting in clones; 3) amphitoky: a rather peculiar trait combining both thelytoky and arrhenotoky in one species.

The advantage of sexual reproduction over asexual reproduction is in the exchange of alleles which results in combinations of genetic material that may be more favourable for survival. In a variable biotope, genetic variation provides a chance that at least some of the offspring are well adapted to the environmental circumstances at a particular time. Diploidy of sexually reproducing animals can also mask recessive mutations (or chromosomal alterations), resulting in a greater genetic variability, which may be of possible future benefit.

In arrhenotoky such a masking is impossible because in the haploid male any mutation unfavourable at a particular time finds expression and consequently disappears (Helle 1965). So, arrhenotoky results in fast selection and fixation of favourable alleles. Another advantage of arrhenotoky may be in colonization: one unfertilized female in a new place can produce male offspring, which might, depending on the adult female's survival and the male development rate, mate and produce female offspring.

Arrhenotoky occurs among the Mesostigmata in, for example, *Macrocheles muscadomesticae* (Pereira & de Castro 1947), among the Tarsonemida in Tarsocheylidae, Heterocheylidae, Dolichocybidae, Trochometridiidae, Pyemotidae, Acarophenacidae, some Pygmephoridae, some Microdispidae, few Scutacaridae, most Tarsonemidae and Podapolipidae (Lindquist 1986), in Actinedida in Tetranychinae, Eryophioidea, (Jeppson *et al.* 1975), *Cheyletus trouessarti* (Hughes 1976) and among the Acaridida in *Histiostoma feronarium* (Scheucher 1959). In Collembola and Oribatida arrhenotoky does not occur.

Apomictic thelytoky, i.e. thelytoky without chromosome reduction, fusion of nuclei, or any similar phenomenon, may have a numerical advantage above sexual reproduction or arrhenotoky because a female gives rise to only females, instead of also producing unproductive males (Williams 1975, Greenwood & Adams 1987). In a constant biotope it has the additional advantage of minimal genetic loss, with daughters inheriting the apparently favourable genome of their mother, and deviations from it (mutations) are rare. However, in a temporally variable biotope, this may be a disadvantage, like sexual reproduction in a constant biotope, because of the chance of changes of the adapted genome. In the other type, automictic thelytoky,

reduction of chromosome numbers takes place and the haploid nuclei may fuse into diploid nuclei (Oliver Jr et al. 1973), resulting in some genetic variation among the progeny, though usually less than in sexual reproduction (Wrensch et al. 1994). Data on the occurrence of each of the types of thelytoky, are sparse. Taberly (1987b) gives evidence for the occurrence of thelytoky of the automictic type in *Platynothrus peltifer* and *Trhypochthonius tectorum* and maybe this type of thelytoky is common among these primitive oribatid mites. Recently, Palmer and Norton (1990) published experimental proof of thelytoky in fifteen species of primitive Oribatida (Desmonomata), but did not mention the type. There are no data on the type of thelytoky in the Mesostigmata (Walter & Oliver 1989).

Thelytoky occurs, for example, among the Oribatida in *Platynothrus peltifer*, *Trhypochthonius tectorum* (Taberly 1987a), *Tectocepheus velatus* (Grandjean 1941), *Oppiella nova* (Woodring & Cook 1962, sub *Oppia neerlandica*) and *Micropia minus* (Luxton 1981); among the Collembola in *Isotoma notabilis*, *Isotomiella minor* and some Tullbergiinae (Petersen 1980); among the Mesostigmata in *Uropoda minima* (Athias-Binche 1981), *Rhodacarus denticulatus* and *Protogamasellus mica* (Walter & Kaplan 1990); among the Actinedida in *Bryobia praetiosa*, *Brevipalpus obovatus* (Jeppson et al. 1975), *Tetranychopsis horridus* (Helle & Bolland 1967) and *Cheyletus eruditus* (Hughes 1976); and among the Tarsonemida in the amphitokous species listed below, and in *Tarsonemus virgineus* (Lindquist 1986).

Amphitoky seems a suitable trait for the colonization of rather constant biotopes: arrhenotoky for a fast selection of the genome adapted to the new environment and thelytoky to quickly populate this environment. In a comparable way the sexual reproduction of the overwintering generation of species that reproduce by thelytoky in the summer can be understood. The best adapted genome of the next summer season is thereby selected and throughout the favourable season the species exploits the biotope most efficiently by reproducing thelytokously, as in holocyclic aphids (Heie 1980) and cladocerans (Ruvinsky et al. 1978). In Rotifera, thelytokous generations during summer are alternated by an arrhenotokous generation in autumn (Allan 1976). It is not known whether a seasonal pattern also occurs in mites. Data on this alternation of reproduction traits are lacking, but the phenomenon may be expected in some tarsonemid or eryophiid mites, because in these taxa both thelytoky and arrhenotoky occur.

Amphitoky has, for example, been observed in *Tarsonemus* (= *Phytonemus*) *pallidus* by Karl (1965a), in *Tarsonemus* (= *Iponemus*) *confusus* by Karl (1965b) and in *Tarsonemus fusarii* by Schaarschmidt (1959); the first eggs laid by the female were reported to give rise to males, later ones to females.

The suitability of the various reproduction traits in space and time is summarized in Figure 2.1.

		Persistence of population	
		maintenance	establishment
Persistence of biotope	constant	thelytoky	sexual reproduction (arrhenotoky)
	variable	sexual reproduction	arrhenotoky (sexual reproduction)

Figure 2.1. Types of reproduction placed in a quadrant containing the persistence of population and biotope.

Semelparity and iteroparity

In addition to the kind of reproduction, the way of oviposition is an important life-history trait. Here, iteroparity, spreading oviposition in time, is compared to semelparity, oviposition on one occasion.

Iteroparity in microarthropods may be assumed to be the basic form of oviposition. The reasons for this assumption are: that it does not imply the need for (1) morphological adaptation (such as physogastry, *i.e.* swelling of the abdomen), (2) a high energy expenditure that comes with the production of offspring in a short period, which could affect survival (such as in semelparity) and (3) extra overwintering or oversummering with the risk of not reaching the next favourable season (such as in seasonal iteroparity). Derivation of this basic type either in the direction of semelparity or of seasonal iteroparity (Bell 1976) would require extra investments, which will only pay off when they lead to an increase in individual survival.

Semelparity in microarthropods limits the oviposition period to the most favourable part of the season or of the life cycle of the host, as in *Iponemus* species parasitizing eggs of the bark beetle *Ips* (Lindquist & Bedard 1961). Another advantage may be the resulting aggregation of offspring which might help decrease water loss in vulnerable individuals just after hatching or moulting (Joose & Verhoef 1974). A disadvantage is that the risk of egg predation may be higher than with iteroparity. A disadvantage of iteroparity is the uncertainty whether the total reproductive capa-

city will be used. Charnov and Schaffer (1973) point out that iteroparity is associated with a relatively long adult lifetime with low mortality. Reduction of the age when the first reproduction takes place, which benefits semelparity (Cole 1954), will be dealt with in the section on development.

Derivations of the basic (iteroparous) form are not very common. The vast majority of microarthropods have an oviposition pattern between semelparity and seasonal iteroparity. Semelparity is found for instance in physogastric Tarsonemida such as *Siteroptes graminis* (Krczal 1959). Adult female physogastry occurs in Pyemotidae, Dolichocybidae, Trochometriviidae, Acarophenacidae, some Pygmephoridae and Podapolipidae and a few members of Microdispidae, Scutacaridae, and Tarsonemidae, for instance the genus *Iponemus* (Lindquist 1986). Tendencies to semelparity, expressed as increasing numbers of eggs per batch, occur to some extent in Collembola. Synchronization of reproduction of a whole population occurs definitely in Collembola: in *Orchesella cincta*, moulting is synchronized after a period of starvation and renewed food availability and with moulting, reproduction is synchronized (Joosse 1969, Joosse & Veltkamp 1970).

At the other end of the gradient, *Neoribates gracilis* may be found; this oribatid mite has a very long adult lifetime (Travé & Duran 1971) and may reproduce in several years. Apart from *Neoribates gracilis*, seasonal iteroparity only occurs in a small number of oribatid mites.

DEVELOPMENT

Development time can take as little as three days up to even three years and depends partly on environmental factors such as temperature and quality of food, but with a strong genetical basis even in geographical forms of a species. Also, a relationship between age of maturation and clutch size has been described (Cole 1954). Variations in developmental time induced by the environment are smaller than variation in the development time of microarthropods within families or orders.

The genetic templet of the higher taxa

In mites the typical development stages (or stases) are egg, larva, protonymph, deutonymph, tritonymph, and adult. This is found in Oribatida, Acaridida and many Actinedida. Mesostigmata lack the tritonymph stage, in Actinedida often only two free nymphal stases are found (Rhaphignatoidea, Tetranychoida, Cheyletoidea) and sometimes even only one nymph is found

(Eriophyoidea and Trombidoidea). Tarsonemida lack all nymphal stases and thus only go through the larval stage. Further reduction in free-living juvenile stases is found in parasitic mites, such as Podapolipodidae where adults hatch directly from the egg, and in a number of species of the Acarophenacidae, Pyemotidae and Dolichocybidae where adults are born from adult females (Van der Hammen 1972, Lindquist 1986). Juvenile stases may not be dropped entirely, as in many species the "missing" juvenile stage is a calyptostase, developing and moulting within the previous stage. The pre-larva in Actinotrichida is always a calyptostase, as are the proto- and tritonymph in Hydrachnellae and Trombidoidea. An intermediate form, free-living but not very mobile on its own, is called the elattostase, such as some of the hypopi (deutonymphs) in Acaridida. It is not likely that the occurrence of calyptostases or elattostases speeds up development. The function of the kind of development is probably synchronization (inert hypopus of *Acarus immobilis*) or dispersal (active hypopi in many other Acaridida), which will be dealt with in the next sections.

Food quality and temperature

The magnitude of variations in development time within a species caused by differences in the quality of food is limited. Stefaniak and Seniczak (1981) found a 1.4 times faster development in *Oppia nitens* on the fungus *Penicillium spinulosum* than on *Cladosporium herbarium*. Walter *et al.* (1987) found in *Gamasellodes vermivorax* and *Cosmolaelaps vacua* a respectively 1.4 and 1.2 times faster development with nematodes than with arthropods as food. Temperature has a more obvious effect on the rate of development. In *Hypogastrura denticulata*, Hale (1965b) found a 2.1 times faster development during the first five moults at 15°C than at 8°C. In Mesostigmata, *Hypoaspis aculeifer* takes 30-33, 13-20, 11-19 and 5 days for development at 13°, 18-20°, 24° and 28°C, respectively (Karg 1971). Fashing (1979) lists development times at various temperatures of three acaridid mites: *Tyrophagus putrescentiae*, *Caloglyphus anomalus* and *Naiadacarus arboricola* at various temperatures. An increase in temperature from 20° to 25°C will speed up development in *T. putrescentiae* 1.3 times, in *C. anomalus* 1.2 times, and in *N. arboricola* 1.8 times. For Oribatida examples of temperature-dependent development are given by Nannelli (1975) for *Oppia concolor*, Bhattacharya *et al.* (1978) for *Oppia nodosa* (= *Lancelaimoppia nodosa*) and Travé and Duran (1971) for *Neoribates gracilis*. In Tarsonemida data for *Steneotarsonemus spinki* are presented by Chen *et al.* (1979) and in Actinedida for *Tetranychus mcdanieli* by Tanigoshi and Logan (1979). Thus, both temperature and food quality influence the rate of development in a species, but these differences are smaller than differences between species from the same taxonomical order. In Oribatida development at 18°C

ranges from 33 days in *Oppia concolor* (Nanneli 1975) to 400 days in *Steganacarus magnus* (Webb 1977). Fashing (1979) gives an example of a comparatively slow developing acaridid species *Naiadacarus arboricola* takes 17.2 days for development while *Caloglyphus berlesei*, *C. anomalus* and *Tyrophagus putrescentiae* need 5.4, 5.7 and 7.3 days at 25°C, respectively. *Naiadacarus arboricola* has in common with *S. magnus* the comparatively low quality of food it uses in its biotope. Most species are unable to change to other food sources (Chapter 4). So, food quality might both have a direct effect on development time and act as a selective force; the price of using the low quality food is a slower development. Thus microarthropods ingesting food which is hard to obtain, or only available in small amounts, or difficult to digest may need a comparatively longer time for development. On the other hand, fast development is only possible when food is abundant and of high quality. An example is *Macrocheles muscadomesticae*, which needs three days to develop from egg to adult (Wade & Rodriguez 1961). This species is synchronized with its carrier (see section on dispersal). Sufficient data lack to present reaction norms (Stearns 1992: the response of the organism to environmental variation), but from the variety present data clearly show it is not unlikely that reaction norms may be crossing. It means that species A may develop in environment a faster than species B,

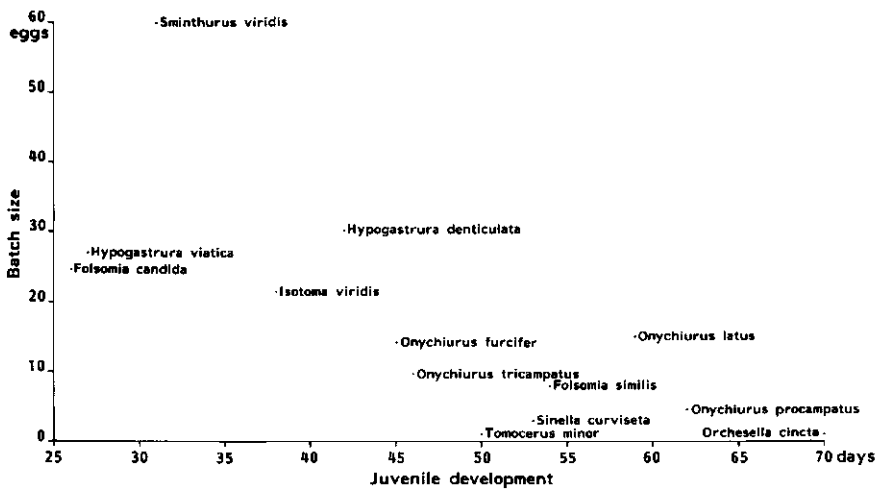


Figure 2.2. Age at first reproduction plotted against batch size in *Collembola* at 15°C. Data are from Davidson (1934), Hale (1965a), Hutson (1978), Jooisse and Veltkamp (1970), Mertens et al. (1983), Niijima (1973), Sharma and Kevan (1963), Snider (1983) and Witteveen and Jooisse (1987).

but in environment b slower than species B. This precludes the use of this trait in a classification.

Relation to semelparity

Minimizing age at first reproduction benefits semelparity and large clutch size (Cole 1954). So, are species with a short development period less iteroparous than others? In gamasid mites, females usually carry only one egg (Karg 1971), but the fast developing *Arctoseius cetratus* (12.5 days from egg to adult at 22°C: Binns 1974) yields a highest daily total of 13 eggs per female (mean 2.5 eggs.female⁻¹.day⁻¹ (Binns 1974)). On the other hand, *Pergamasus robustus* takes on average 43.5 days from egg to adult and the oviposition period is quite long, yielding an egg production of 0.25 egg.female⁻¹.day⁻¹ (Bhattacharyya 1963). For Collembola, age at first reproduction at 15°C in laboratory experiments is plotted in Figure 2.2 against the number of eggs per batch at the same temperature. The relationship is significant (linear regression: $p < 0.05$) for species for which values could be obtained. Note the difference in the definition of batch as the number of eggs deposited at the same time at the same place, and that of clutch in Van Straalen and Joosse (1985) and Janssen and Joosse (1987) as the number of eggs laid during a reproductive instar period. These clutch values are usually bigger, and may consist of several batches, with a considerable variation in hatching time.

Hence, in Collembola a relationship exists between minimizing age at first reproduction and a less iteroparous reproduction.

SYNCHRONIZATION

The life cycle of a species can be synchronized with the environmental factors most important for that species. These environmental factors can be abiotic, synchronizing the life cycle with the cyclic period in the environment, or the "environmental" factors may be biotic; synchronizing the species' life cycle with that of its carrier (in phoretics) or host (in parasites) thus being not necessarily seasonal. I will focus here on seasonal synchronization and deal with synchronization to carriers in the section on dispersal. Resting stages can be quite primitive, known as non-diapause dormancy, or have a solid physiological basis, called diapause dormancy.

Non-diapause resting stages

Species have developed all kinds of solutions for overcoming unpredictable

or predictable unfavourable periods in the environment, such as moving on and settling elsewhere or withstanding harsh conditions. Microarthropods hardly migrate. The locomotory capacity of most species is low. Vertical movement, however, does occur and is a way of escaping from desiccation, or from very low or high temperatures (Metz 1971).

Some Collembola, Oribatida, and Actinedida have developed the ability of supercooling, a physiological process of accumulation of polyols (glycerol) in the haemolymph, which gives the animal a better chance of surviving temperatures below the freezing point of their haemolymph (e.g. Sømme, 1981). These species are primarily (ant)arctic or alpine, but also the temperate Oribatida *Carabodes labyrinthicus*, *Fuscozetes fuscipes* and *Ceratopia bipilis* are among those listed by Sømme (1981). A long period under harsh conditions without food will evolve to quiescence, which is defined by Tauber *et al.* (1986) as "a reversible state of suppressed metabolism imposed by conditions beyond certain thresholds in temperature, moisture and nutrition". Whenever quiescence has a seasonal basis it is called non-diapause dormancy (Tauber *et al.* 1986), occurring for instance in the oribatid *Alaskozetes antarcticus* (Young & Block 1980). Mesostigmatid mites generally have continuous generations, but in the terrestrial mesostigmatid *Zerconopsis müstairi* the eggs can overcome a long period of fresh-water submergence (up to 128 days). The same holds for the actinedid *Cheylostigmaeus pannonicus* and some Collembola (Tamm 1984). Acaridid mites overcome harsh periods as hypopi (deutonymphs), for example *Acarus immobilis* (Hughes 1976).

Diapause dormancy

Real diapause to overcome a harsh season is rather uncommon in soil microarthropods. Where it occurs, diapause dormancy has evolved in usually one but in some cases more life stages. In Collembola some species overwinter as diapause eggs (Blancquaert *et al.* 1981), but most, especially euedaphic, species have continuous generations and no diapause at all, comparable to most oribatid mites. In Tarsonemida, adult females overwinter (Lindquist 1986), but it is not clear whether this is a real diapause. The very heterogeneous actinedid mites have various ways of overcoming a harsh season. In some species of Eryophyoidea, the normal females alternate with deutogynes in a harsh season. These deutogynes occur in species from temperate and arctic latitudes and have to be subjected to winter chilling before they can reproduce: a real diapause dormancy (Jeppson *et al.* 1975). Also the Tetranychidae and mites of some other families, pass the unfavourable season as adult females, but some tetranychids and some species from other families overwinter as diapause eggs (Jeppson *et al.* 1975).

Summer diapause or aestivation occurs in the egg stage in Eupodoidea (*Halotydeus destructor*) (Wallace 1970) and in Tetranychoida (*Petrobia*

latens) (Jeppson *et al.* 1975) among the Actinedida. In Collembola Najt (1983) and Joosse (1983) reported ecomorphosis in Hypogastruridae and Isotomidae: adults show morphological and physiological changes, creep away in deeper soil layers and starve. Barra and Poinso-Balaguer (1977) described another adult adaptation to summer drought in Collembola: anhydrobiosis. In contrast with ecomorphosis, anhydrobiotic animals become active as soon as soil moisture conditions are favourable again. However, most species overcome the dry season in the egg stage.

DISPERSAL

In microarthropods dispersal by active locomotion is of minor importance compared with dispersal by wind (anemochory), by water, or by animal carriers, mostly insects (phoresy). Zachvatkin (1959) measured $5.2 \text{ mm} \cdot \text{min}^{-1}$ for *Caloglyphus rodionovi* (= *C. berlessei* (Michael 1903)) up to $150 \text{ mm} \cdot \text{min}^{-1}$ for *Glycyphagus* (= *Lepidoglyphus*) *michaeli* (Oudemans 1903). Many predators (Gamasina and Actinedida) move faster but their movements are seldom in a straight line, thus covering short distances only.

Phoresy or anemochory are life-history traits to be considered in the classification of life-history tactics. Unlike phoresy, anemochory will be associated with high egg production. Mitchell (1970) ranks *Tetranychus* - *Poecilochirus* - *Iponemus* (resp. anemochoric, phoretic carrier-unspecific, and phoretic carrier-specific) according to the probability of discovering a new resource. Phoresy has not yet been recorded in Collembola, thus the next section only deals with mites.

Phoresy

Farish and Axtell (1971) define phoresy as the "phenomenon in which one animal actively seeks out and attaches to the outer surface of another animal for a limited time during which the phoretic ceases both feeding and ontogenesis, such attachment presumably resulting in dispersal from areas unsuited for further development, either of the individual or its progeny". In some occasions the phoretic may have been observed feeding on the carrier (Jalil & Rodriguez 1970). It is questionable whether phoresy is always initiated by an expected degradation of the biotope, as many phoretics live in biotopes that exist longer than one generation period (for instance, nidicolous and corticolous species).

Dispersal in mites may occur in very specific ways. When a mite attaches to a host (mostly an insect), that carries it to another place, the mite

is called the phoretic and the host is called the carrier. Binns (1982) reviews phoresy extensively. Here, I consider only a few of its ecological aspects: the life stage of the phoretic, whether or not synchronisation with its carrier takes place, whether or not the phoretic is carrier specific, and whether phoresy is obligate, facultative or just accidental. In many papers (cf. Binns 1982), accidental phoresy refers to the relationship between the phoretic and the carrier. However, I use accidental phoresy to express the phoretic movement of a species that is seldomly phoretic.

Life stage of the phoretic

Without exception, in Uropodina the phoretic is the deutonymph (Athias-Binche 1984) which has developed a flexible stalk at the rear end of the hysterosoma. Not all uropodids are phoretic (Athias-Binche 1981), for example, some soil inhabitants of the genera *Trachytes*, *Polyaspinus* (all species) and *Dinychus* (some species). For a detailed description of the uropodid deutonymphs see Karg (1989). Also in the Acaridida the phoretic is the deutonymph, called the hypopus, which is also specially adapted to cling on a carrier as described in detail for many species by Hughes (1976). Again not all hypopi among the Acaridida are phoretic; some hypopi are inert resting stages. They are highly resistant to desiccation (Griffiths 1964) and other forms of stress. *Carpoglyphus lactis* (Linnaeus 1758) can even pass through the alimentary canal of mice and sparrows (Chmielewski 1970). The best-fitted organism to found a new colony is a non-gravid fertile female (Southwood 1962, Binns 1982). Adult phoretics are usually females (Jalil & Rodriguez 1970). Especially in the Tarsonemida, phoresy occurs in this life-stage (Lindquist 1986). Finally, in the Gamasina, phoresy may occur in either the adult life stage, for example, *Macrocheles* spp. (Jalil & Rodriguez 1970, Krantz & Whitaker 1988) and *Arctoseius cetratus* (Binns 1974), or in the deutonymph as in *Digamasellus* (= *Dendrolaelaps*) *fallax* (Leitner 1949) (Binns 1973) and *Parasitus* spp. (Karg 1971). Further information on associations between Mesostigmata and other arthropods including parasitism can be found in Hunter and Rosario (1988). In the Oribatida and Actinedida in which phoresy occasionally occurs, the phoretics are generally adults (Desender & Vanechoutte 1984, Norton 1980).

Synchronization of phoretic and carrier

Lindquist (1975) distinguishes four types of synchronization between phoretic and carrier, all of them adaptations of the mites. In the first type, the life cycle of the mite is restrained during an early period of the life cycle of the carrier; during the egg and larval development of the carrier, the adult female mite undergoes an inactive post-phoretic period. During

the prepupal stage of the carrier, these female mites become active, seem to feed on cuticular exudates, lay eggs which develop during the pupal stage of the carrier to young females, which leave the nest with the new generation of carriers. Skaife (1952) describes an example of this with *Dinogamasus braunsi* on the carpenter bee *Mesotrichia caffra*. Of course, in this relationship phoresy is obligate and specific.

The second type of synchronization is characterized by a restraint during a late period in the life cycle of the carrier. The female phoretic starts laying eggs at the same time as its carrier and feeds on its carrier's eggs. The eggs and larvae quickly develop into a new generation of young mites, which wait 3-6 weeks without feeding. This type of synchronization is documented by Lindquist (1969) for several species of *Iponemus*, which are all very carrier specific and obligate phoretics on ipine bark-beetles.

The third type of synchronization is the interruption of the mite's life cycle during a period between the generations of a carrier. The phoretic here is the juvenile stage (deutonymph or hypopus) waiting for a carrier. The relationship is not necessarily carrier specific, and deutonymphs can attach to any organism entering the biotope (Binns 1972) and also the deutonymph stage can be omitted, thus resulting in facultative phoresy (Binns 1982).

The fourth type of synchronization is a race against time. *Macrocheles muscadomesticae* develops in three days from egg to adult and its main carrier *Musca domestica* takes two days to reach the second instar, which is immune to predation by the mites, that feed on the eggs and first instar larvae of the fly (Wade & Rodriguez 1961).

Obligate and facultative phoresy and carrier-specificity

In phoresy, a trend can be observed from occasional transport to regular transport diverging into two pathways. The first is carrier unspecific biotope-dependent such as in *Arctoseius cetratus*, an adaptation ending with the synchronization in development of *Macrocheles muscadomesticae* with flies such as the housefly (Wade & Rodriguez 1961), one out of more than a dozen of carriers (Hunter & Rosario 1988). The other is carrier specific, ranging from species sharing the same biotope as the carrier, such as in *Dinogamasus braunsi*, which feeds on the eggs of its carrier and remains a relatively short period on the carrier (Skaife 1952), to species which are called parasites, only leaving the host to reproduce, or even reproducing on the host itself, such as in *Sarcoptes* spp. and *Demodex aurati* (Nutting 1964) in the Acaridida, and Spinturnicidae (Sweetman 1971) in the Mesostigmata. Species of the latter categories may show some parental care in the form of larviparity (Dolichocybidae, Pyemotidae and few Pygmephoridae among

the Tarsonemida) (Lindquist 1986) or even give birth to adults (Acarophenacidae in the Tarsonemida, such as *Acarophenax tribolii*) (Hughes 1976).

Phoresy in the case of *Musca* and *Macrocheles* is obligate, as the biotope does not exist long enough for the development of more mite generations, but probably not carrier specific. The fast development of the mite is favoured by high quality of the food (see the section on development). The function of the fast development of the fly during the egg stage and first larval instar seems to escape from acarine predators occurring in such biotopes. Among oribatid mites phoresy is probably accidental; hardly any species relies on phoresy in its life history. Exceptions may be the wood inhabiting oribatid mites listed as phoretics by Norton (1980), especially the *Mesoplophora* spp., clinging to insect hairs. A parallel may be found in *Naiadacarus arboricola* that lives in waterfilled tree-holes (Fashing 1975) and other inhabitants of discrete biotopes such as nests of mammals, birds, and ants. Phoresy in these cases may be facultative, because the biotope remains intact for several generations, and is not necessarily carrier specific. In Actinedida mites of the family Cheyletidae are phoretic (Van Eynhoven 1964) such as *Cheyletomorpha lepidopterum* (Shaw 1794), which is phoretic in the adult stage and phoresy is probably facultative and not carrier specific.

		Persistence of population	
		continuous	discontinuous
Persistence of biotope	continuous	continuous generations	diapause or quiescence
	discontinuous	facultative phoresy	anemochory obligate phoresy

Figure 2.3. Types of synchronization and dispersal in microarthropods placed in a quadrant containing persistence of population and biotope.

Analogous to Southwood's (1977) time-space quadrant, Figure 2.3 shows a time-biotope quadrant with traits that may have survival value under discontinuity either in biotope, or in time. Species living in continuous bio-

topes, such as forest soils, need no special adaptations in their life history in terms of diapause (to bridge an unfavourable part of the season) or migration (to bridge an unfavourable space to the next favourable biotope). If the persistence of the population is discontinuous, i.e. when unfavourable conditions during part of the year exist, then adaptations such as diapause or quiescence have survival value. Discontinuities in the biotope can be solved by migration in microarthropods, especially by phoresy. Phoresy, combined with comparatively stable biotopes (continuous and overlapping in time), can lead to carrier-specificity, possibly with egg parasitism. Time spent on the carrier is relatively short, as in *Vidia concellaria* (McNulty 1971) and in *Dinogamasus braunsi* (Skaife 1952), and always predictable. Biotope examples are decaying wood, and nests of ants, birds, and mammals. Discontinuity in both time and biotope refers to ephemeral biotopes such as carrion and dung-patches. Phoresy here is likely to be un-specific, e.g. in *Macrocheles muscadomesticae* (found on 16 dung-visiting fly species; Hunter and Rosario 1988) although a synchrony has evolved with the development of its main carriers. Time spent with the carrier may be either long or short, but is unpredictable. For example, *Poecilochirus necrophori* is phoretic on both the carrion beetles *Necrophorus humator* and *N. investigator*; deutonymphs stay in the pupal cell of the carrier during a pupation of either 2 (*N. humator*) or 10 months (*N. investigator*) (Springett 1968). *P. necrophori* may be an example of what Stearns (1976) called species adapted to noncyclic biotopes, i.e. biotopes distributed as random variables in time.

Anemochory

Another major form of dispersal, anemochory, is found in the Actinedida, especially in the Tetranychoida and Eriophyoidea (Jeppson *et al.* 1975). Compared to phoresy, where the phoretic is usually carried to a new exploitable biotope, in anemochory the loss of individuals which do not reach a new favourable biotope is reported to be over 90 per cent (Jeppson *et al.* 1975). These anemochoric species will generally have a higher reproductive rate than phoretics; for example, *Tetranychus urticae* Koch produces 90-110 eggs per female (Jeppson *et al.* 1975), and the phoretic *Dinogamasus braunsi*, 5-10 eggs per female (Skaife 1952).

BOUNDARIES AND TRANSITIONS

It is clear from the previous sections that a life-history trait cannot

easily be called r-selected or K-selected. The way the trait is used determines how it fits into the tactic as a whole; it can be used as an answer to completely different environmental problems. Phoresy for instance is commonly seen as a 'r-selected' trait (Binns 1982; Hunter & Rosario 1988) but most of the carrier-specific facultative phoretics in Figure 2.3 have a rather low egg production and often other traits that would classify them as K-, rather than r-selected (Fashing 1975, 1979; reporting on *Naiadacarus arboricola*). Likewise, *Mesoplophora* spp. do not show r-selected traits, but nevertheless are phoretic (Norton 1980). So phoresy seems to be an answer both for rapid colonization and exploitation of ephemeral biotopes occurring randomly in time and place, and for colonization of discretely distributed biotopes, which may persist for many generations of microarthropods.

The slow development of *Naiadacarus arboricola* may in part be an adaptation to the limited food resources as indicated for many Oribatida in the section on development. In these circumstances the slow development trait can hardly be considered K-selected, as Fashing (1979) does, because the limited food quality is not due to competition. Rather it should be called S-selected in the sense of Grime (1979), because it is an adaptation to a harsh aspect of the environment.

Low temperature, another harsh aspect of the environment, also leads to slow development. Even quiescence forms, such as some hypopi in the Acaridida or some deutonymphs in the Mesostigmata, may be classified as forms of slow development. Again this is an example where the function of one trait, slow development, can be to meet different environmental problems: a cold period, a dry period, or low food quality.

Different answers for the same environmental problems are well known. Solutions to environmental changes are either migration, or diapause or a combination of both, depending on the reversibility and regularity of the environmental changes (Southwood 1962). Regular changes lead to diapause forms and irregular changes to migration. Another example of a different answer to the same environmental problem may be seen in migration itself. A favourable biotope for the continued existence of a population may be reached by random migration accompanied by a high reproductive rate associated with a high number of casualties, or by directional migration, as in phoresy, which is only accompanied by a high reproductive rate when the favourability of the new biotope is uncertain.

Hence, it would seem that simple systems to represent life-history tactics such as the one-dimensional continuum of the r- to K-axis (MacArthur & Wilson 1967) or the two-dimensional systems of the R-, C- and S-triangle (Grime 1977, 1979, Grime *et al.* 1988) and the space-time quadrants (Southwood 1977) are too simple.

The multidimensional system of Stearns (1976) is not suitable to represent the life-history tactics of microarthropods either. Multivoltinity is

presented as an adaptation to environmental cycles much longer than the lifespan. Examples of univoltine insects are given when the cyclic period is about equal to or shorter than the lifespan. This suggests that voltinicity is an important trait. The number of generations per cyclic period (usually a year in temperate regions), however, is not a trait in itself, but is derived from development and synchronization. For example, a species univoltine in temperate regions, would only stay univoltine in subtropical and tropical regions if its life cycle had an obligate diapause, and in boreal regions if its development was fast enough to complete the life cycle within a year. Species subject to facultative diapause (Tetranychidae) or without any diapause (Oribatida) may be univoltine in boreal regions, sometimes even taking more than one year to complete their life cycle, and multivoltine in temperate, subtropical, or tropical regions. Thus the number of generations per cyclic period can only be used as a life-history trait for classifying life-history tactics when it is accompanied by an obligate diapause and is thus restricted to the use of obligate univoltinity, or bivoltinity when an obligate aestivation forms part of the life cycle.

In conclusion, low dimensional schemes of life-history tactics appear to be too simple and the only multidimensional scheme presented in the literature (Stearns 1976) is not well defined in all respects and is consequently of limited use to represent life-history tactics of microarthropods. Therefore, a different scheme of microarthropod life-history tactics is designed below.

LIFE-HISTORY TACTICS

Twelve life-history traits of microarthropods are distinguished: sexual reproduction, thelytoky, amphytoky, arrhenotoky, iteroparity, semelparity as reproductive traits; the relative rate of development as developmental trait; obligate diapause, facultative diapause and quiescence as synchronization traits; and phoresy and anemochory as migration traits. The best way to make such a classification is to analyse all traits thoroughly and build up the tactics trait by trait (Harvey & Pagel 1991, Stearns 1992). However, in a field where specified data on life-history traits are scattered I followed an iterative method. For every imaginary tactics species examples were to be found and finally any species had to be placed in a tactic without difficulties. For instance, there are no microarthropod species combining the traits adult obligate phoresy with thelytoky. This method resulted in twelve life-history tactics (Table 2.1). The sequence of traits as presented in Figure 2.4 is not meant to be hierarchical.

Table 2.1. Life-history tactics derived from life-history traits

Tactic	zoobiont (fully/partly)	phoresy (facultative/ obligate)	anemochory	diapause (obligate/ facultative/ quiescence)	sexual reproduction	thelytoky
I a	fully	-	no	no	yes	no
b	partly	-	no	quiescence may occur	yes	no
II	no	facultative or when obligate then carrier-specific	no	may occur	yes	occurring
III	no	obligate in juve- niles, possessing morphological and physiological adaptations	no	quiescence	yes	no
IV	no	obligate in adults	no	quiescence	yes	no
V	no	no	no	obligate (and/or additional obligate aestivation)	yes	may occur
VI	no	no	no	facultative or quiescence	yes	may occur
VII	no	no	yes	facultative or quiescence	yes	no
VIII	no	no	no	facultative or quiescence	yes	may occur
IX	no	no	no	quiescence	no	yes
X	no	no	no	no	no	yes
XI	no	no	no	no	yes	no
XII	no	no	no	no	yes	no

continuation of Table 1

	amphytoky	arrhenotoky	semelparity	iteroparity (continuous/ seasonal)	egg production	viviparity (parental care)	development
I a	no	no	no	continuous	low	occurring	moderate
b	no	no	no	continuous	low	occurring	moderate
II	rarely	occurring	may occur	continuous	low	occurring	slow
III	no	occurring	may occur	continuous	high	occurring	fast
IV	no	occurring	may occur	continuous	high	may occur	fast
V	no	no	may occur	continuous	moderate	may occur	slow to fast
VI	no	may occur	yes	no	high	may occur	fast
VII	no	occurring	no	continuous	high	may occur	fast
VIII	no	no	no	continuous	moderate	may occur	fast
IX	no	no	no	continuous/ seasonal	low to moderate	may occur	slow
X	no	no	no	continuous	moderate	no	quite fast
XI	no	no	no	continuous	moderate to high	no	quite fast
XII	no	no	no	seasonal	moderate	no	slow to quite fast

Microarthropod communities

zoobiont	<ul style="list-style-type: none"> - fully zoobiont - partly zoobiont 		
phoretic	<ul style="list-style-type: none"> - facultative (mostly carrier specific) - obligate (mostly carrier unspecific) 	<ul style="list-style-type: none"> - as juvenile morphological and physiological adapted - as adult without special adaptations 	
not phoretic	<ul style="list-style-type: none"> - synchronization - no synchronization 	<ul style="list-style-type: none"> - obligate diapause - facultative diapause or quiescence - thelytokous - sexual reproduction 	<ul style="list-style-type: none"> - semelparous - iteroparous - anemochorous - not anemochorous - slow development - fast development - continuous iteroparity - seasonal iteroparity

Figure 2.4. Scheme of microarthropod life-history tactics as they are defined by the main life-history traits.

The limited number of life-history tactics recognized and the relative insensitiveness to the rank order of traits distinguished implies a high degree of correlation between traits.

THE MAIN BIOTOPES PER TACTIC AND SPECIES EXAMPLES

The main biotopes of species with the life-history tactics distinguished above, will be dealt with briefly. Tactics are assembled in three groups

for convenience: directional dispersal, synchronization, and reproduction tactics, named after their most significant traits.

Table 2.2 gives examples of the tactics at the species level within the main orders of the Acari (Acaridida, Oribatida, Actinedida, Tarsonemida, Mesostigmata) and the insect order Collembola. Table 2.2 shows that Collembola is the most homogeneous order with respect to life-history tactics and that the mite orders Actinedida and Mesostigmata are the most heterogeneous. Inclusion of Collembola does not lead to any additional tactics. Collembola generally have a relatively fast development and the only other life-history traits developed are thelytoky, in a large number of species, and diapause eggs, in a small number of species.

For convenience, in the review of the tactics, tactic numbers are preceded by a short, hence incomplete, list of life-history characteristics.

Directional dispersal tactics

Tactic I is confined to parasites of vertebrates and invertebrates. A distinction has been made between those living exclusively on the host (Ia) and those partly free-living for reproduction or dispersal (Ib). The species showing facultative phoresy (tactic II) are generally species of relatively long existing, discretely distributed biotopes. In this case phoresy serves to colonize new biotopes, but leaving the biotope is not obligatory because the biotope will persist for a rather long time. Carrier specificity seems the best means for reaching the biotope. An increase in the development rate is usually not functional, except for achieving synchronization with the carrier, and retarded development may occur because of synchronization, or harsh conditions, such as low food quality. Because of phoresy, species with obligate juvenile phoresy (tactic III) are able to quickly colonize ephemeral biotopes, such as dung pats, carrion, decaying mushrooms, and rotting fruit. Phoresy is obligate due to the transient nature of the biotope, and therefore usually not carrier specific. The same holds for obligate adult phoretics (tactic IV), but the difference between the two is the ability of the adult phoretics to correct their arrival in an unsuitable biotope by taking another carrier to the next biotope.

Parasitic forms occur in all mite orders except Oribatida. Phoresy occurs in all mite orders and is either facultative, or when obligate, then carrier specific, with relatively slow development. Obligate juvenile phoresy with physiological and morphological adaptations is restricted to Acaridida and Mesostigmata, while obligate adult phoresy, mostly carrier unspecific, seems to be restricted to the Mesostigmata.

Synchronization tactics

Species with an obligate diapause (tactic V) are either univoltine or bivoltine (having both an obligate diapause and an obligate aestivation in alternate generations); they are highly synchronized with the season, which is usually accompanied by a high reproductive success. Synchronization with the biotope is realized in two ways in species with a combination of facultative diapause and semelparity (tactic VI). Species with facultative diapause or quiescence (tactic VIII) combined with anemochory (tactic VII) can easily overcome unfavourable periods in the environmental cycle.

Obligate diapause is restricted to the Actinedida and Collembola. Facultative diapause and semelparity occurs in the Tarsonemida and Collembola only. Facultative diapause or quiescence with anemochory occurs in some Mesostigmata and in the Actinedida (Tetranychidae and Eryophiidae). Synchronization in Mesostigmata refers to quiescence and in Tetranychidae to facultative diapause. Sole quiescence or facultative diapause occurs in almost all orders.

Reproduction tactics

The presence of thelytokous reproduction distinguishes tactics IX and X from XI and XII. Species reproducing by thelytoky can be expected in quite constant environments, or environments made constant by human activities by imposing a very harsh and dominant constant factor. Under new conditions, species with thelytoky (tactic X) increase faster than those with thelytoky and seasonal iteroparity (tactic IX); in more established conditions, species with thelytoky overcome disturbance more easily than species with thelytoky and seasonal iteroparity, because of their shorter generation time. There are many species with sexual reproduction (tactic XI) that can be found in almost any biotope in soil or vegetation. Sexual reproduction and continuous iteroparity result in spreading the risk of a complete loss of offspring. Spreading the risk of harsh events is even better in sexually reproducing species with seasonal iteroparity (tactic XII), where the loss of a complete reproductive season may be permitted.

Thelytoky occurs in all the orders listed, although in the Acaridida thelytoky may occur only in combination with facultative phoresy. Sexual reproduction occurs in all orders. Sexual reproduction with seasonal iteroparity seems to be restricted to the Oribatida.

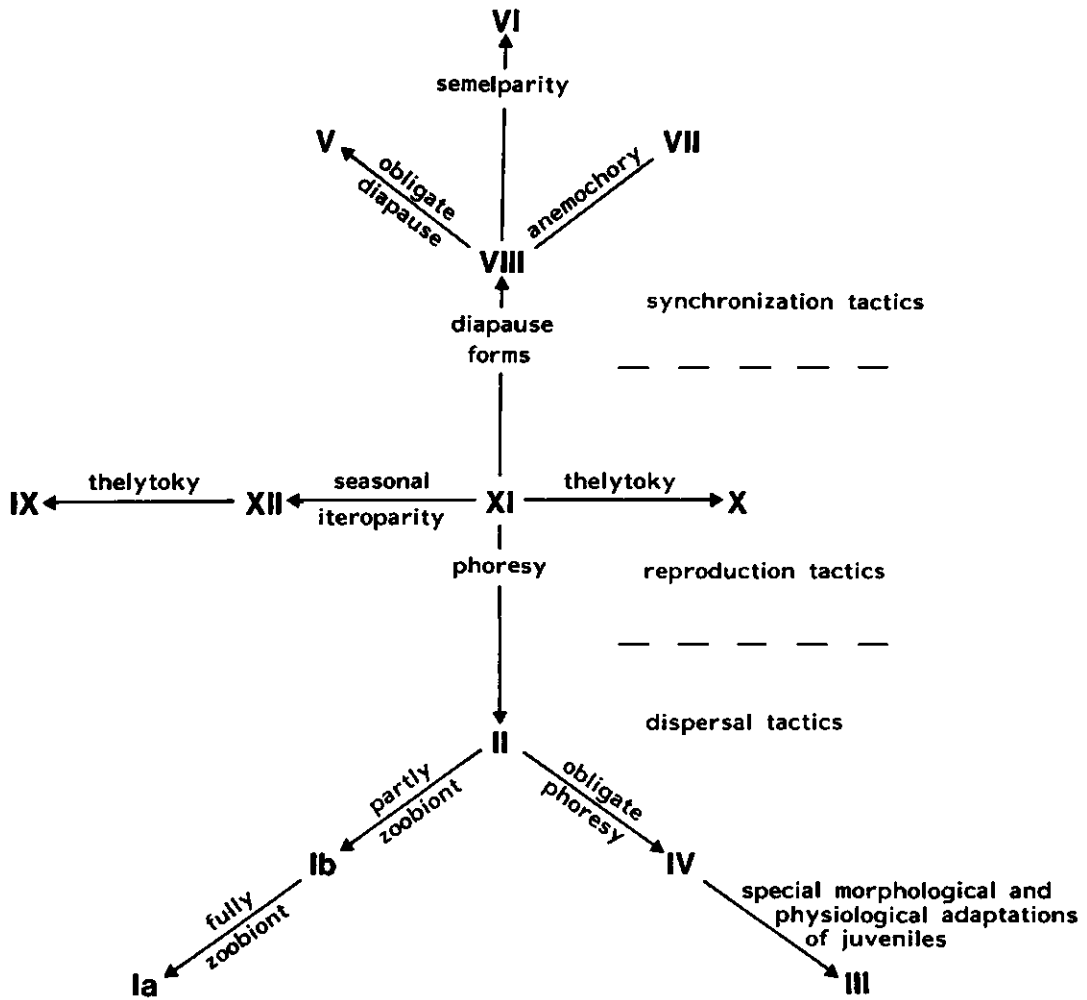


Figure 2.5. Scheme of the interrelationships between the life-history tactics defined for microarthropods. For definition see Table 2.1.

Table 2.2. Species examples from the five large orders of the Acari and the order Collembola for the life-history tactics as defined in Table 2.1.

		Acari					Insecta	
Tactic	Acaridida	Oribatida	Actinedida	Tarsonemida	Mesostigmata	Collembola		
I a	<i>Sarcoptes scabiei</i>	none	<i>Demodex surati</i>	<i>Acarophenax tribolii</i>	<i>Spinthrunix myoti</i>	none		
b	<i>Canestrinia dorcicola</i>	none	<i>Nectrombicula autumnalis</i>	<i>Acarapis woodi</i>	<i>Eulaelaps stabularis</i>	none		
II	<i>Maidsacarus arboreicola</i>	<i>Mesoplophora pulchra</i>	<i>Cheyletus eruditus</i>	<i>Iponemus confusus</i>	<i>Discogamasus braunsi</i>	none		
III	<i>Histioglyphus brevimanus</i>	none	none	none	<i>Parasitus coleoptratum</i>	none		
IV	none	none	none	none	<i>Macrocheles muscadomesticae</i>	none		
V	none	none	<i>Bryobia praetiosa</i>	none	none	none		
VI	none	none	none	<i>Siteroptes graminis</i>	none	none	<i>Sminthurus viridis</i>	
VII	none	none	<i>Tetranychus cinnabarius</i>	none	<i>Amblyseius potentillae</i>	none		
VIII	<i>Acarus immobilis</i>	<i>Alaskozetes antarcticus</i>	<i>Petrobia luteus</i>	none	<i>Zercopsis müstairi</i>	<i>Anurida tullbergi</i>		
IX	none	<i>Nothrus silvestris</i>	none	none	none	none		
X	none	<i>Oppiella nova</i>	<i>Brevipalpus obovatus</i>	none	<i>Trachytes segrota</i>	<i>Folsomia candida</i>		
XI	<i>Tyrophagus similis</i>	<i>Oppia concolor</i>	<i>Tydeus mali</i>	<i>Stenotarsonemus spinki</i>	<i>Hypoaspis aculeifer</i>	<i>Neanura muscorum</i>		
XII	none	<i>Adamaeus onustus</i>	none	none	none	none		

COMPARISON WITH OTHER LIFE-HISTORY TACTICS

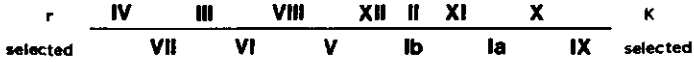
The twelve life-history tactics of microarthropods are schematically shown in Figure 2.5. Except for the classification given by Stearns (1976), general classifications of life-history tactics are of low dimensionality (MacArthur & Wilson 1967, Grime 1977, Southwood 1977). The advantage of these theories is their easy accessibility compared to the more complex scheme (Fig. 2.5). To make the life-history tactics of microarthropods more understandable, they can be projected onto the r-K continuum of MacArthur & Wilson (1967), the triangle of Grime (1977) and the time-space quadrant of Southwood (1977), respectively (Fig. 2.6). The location of a tactic along the r-K continuum or in the triangle depends very much on the weight given to the traits contained in the life-history tactic. Putting the tactics along the r-K gradient, the trend in egg production is generally from high (r-selected) to low (K-selected), but a trait like thelytoky may cause some shifts. In the R-C-S triangle the r-K continuum is extended by the dimension stress-tolerance (S-selection); translated in terms of microarthropod life-history traits, S-selection is comparable to facultative diapause or quiescence, used to bridge harsh parts of the cyclic period, or to seasonal iteroparity that can bridge a lost season. Traits like obligate diapause or semelparity, however, are not only S-selected, and life-history tactics including these traits are placed in the middle of the triangle, which is poorly defined. The quadrant of Southwood (1977) is well defined and traits selected for 'later' are diapause or quiescence and seasonal iteroparity and those for 'elsewhere' are phoresy and anemochory, resulting in the placing of facultative phoretics (II; partially) and facultative diapause with anemochory (VII) in the 'later-elsewhere' section. Although well-defined, the time-space quadrant poorly distinguishes between several tactics, because traits on development and type or rate of reproduction are not considered.

The scheme of environmental characteristics according to Stearns (1976) is filled with the microarthropod life-history tactics (Table 2.3). Stearns' scheme is elaborated in detail for organisms living longer than one cyclic period, but does not discriminate among the tactics of organisms living shorter than the cyclic period. Although developed and defined differently, the scheme of Stearns and the microarthropod life-history tactics may be mutually supplementary, but, as stated in the section on boundaries and transitions, the distinction between univoltine and multivoltine species is subject to criticism.

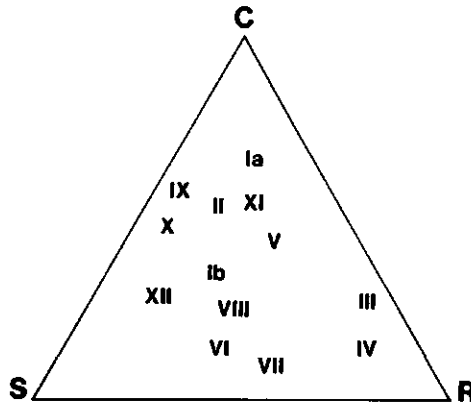
Both Stearns' scheme and the proposed scheme of life-history tactics of microarthropods, are multi-dimensional and thus hard to visualize entirely. Figure 2.5 shows the interrelationships of the life-history tactics of

Microarthropod communities

a



b



c

		Time	
		now	later
Space	here	Ia, IX, X, XI	V, VI, VIII, XII
	elsewhere	Ib, II, III, IV	II, VII

Figure 2.6. Projection of microarthropod life-history tactics on a) the r-K continuum of MacArthur and Wilson (1967), b) the C-S-R triangle of Grime (1977), and c) the time-space quadrant of Southwood (1977). See Table 2.1 for definition of the life-history tactics.

Table 2.3. Environmental conditions according to Stearns (1976) with allocated micro-arthropod life-history tactics.

Environmental conditions	Life-history tactics
1 Cyclic, fixed period period >> life span	I, II, VI, VII, VIII, X, XI
2 Cyclic, fixed period period < life span:	
a. start of cycle and conditions during cycle predictably favourable	V
b. start of cycle predictable within limits, cycle predictably favourable	IX
c. start of cycle predictable, condi- tions during cycle unpredictable; no information on future conditions available at start of cycle	XII
d. as c, but some information available on future conditions	none
3 not cyclic, distributed randomly over time.	III, IV

microarthropods. From the centrally placed sexual reproduction (tactic XI), two main groups of tactics diverge, tactics with phoresy and those with a diapause form (including quiescence), as well as two minor groups of tactics, those with seasonal iteroparity and thelytoky. Further subdivision of the group having diapause forms, discriminates between tactics with semelparity or anemochory. Groups with phoresy can be divided into those with zoobiontic tactics and obligate phoresy. The scheme is not intended to imply phylogenetic relationships.

RELEVANCE TO OTHER ORGANISMS

An interesting point is the generality of the life-history traits on which the tactics are based. Diapause forms (or quiescence) are widespread among insects. In plants the equivalent traits may be seed dormancy and the persistence of seed banks, next to phanerophyte and geophyte life forms. Anemochory is also common in many insects as well as in plants. Directional migration, or phoresy, may be equated with myrmecochory, endozoochory in plants with obligate phoresy (often necessary for germination) and exozoo-

chory with facultative phoresy. Thelytoky and arrhenotoky are not uncommon among insects; thelytoky occurs, e.g., in white flies and aphids (Homoptera: Aphidina and few Aleyrodina), in braconid wasps (Hymenoptera; Braconidae), and in several beetles (Coleoptera; Staphylinidae, Curculionidae), arrhenotoky in several Hymenoptera. Thelytoky also occurs in several other invertebrates such as earthworms (Edwards & Lofty 1972), isopods (Sutton 1972) and nematodes (Bongers 1988). The vegetative reproduction of plants may be compared with apomictic thelytoky and cleistogamy with automictic thelytoky. Vivipary, seen as parental care in microarthropods, may be compared with stolon or rhizome production in plants.

Thus, the life-history traits used in the definition of microarthropod life-history tactics are of general importance (or can be translated to equivalent traits), so a definition of the same tactics using other organisms may be possible. However, not all tactics are likely to have representatives among all kinds of organisms, and new tactics also may have to be defined in situations where examples from microarthropods are lacking, such as thelytoky with a seasonally initiated sexual generation, found in cladocerans (Ruvinsky *et al.* 1978) and aphids (Heie 1980), or thelytoky with a seasonally initiated arrhenotokous reproduction in rotifers (Allan 1976).

DISCUSSION

The traits on which the life-history tactics are based, presented in this paper, are not entirely discrete. Even a seemingly discrete difference such as between sexual reproduction and thelytoky is continuous, if seen on a large scale as in geographic parthenogenesis, or on a smaller scale as environmentally induced female-biased sex ratios. Suomalainen (1950) and Glesener & Tilman (1978) have reviewed geographic parthenogenesis. They concluded that thelytoky occurs at high rather than low latitudes and altitudes, in xeric rather than mesic biotopes, in disturbed rather than undisturbed places and on islands rather than on the mainland. Glesener & Tilman (1978) showed that the cost of meiosis is explained by the biological uncertainty individuals have to cope with. As the biological stress, either a generation later, or in a new biotope, is uncertain, some variation created by outcrossing is favourable. This implies that the biological uncertainty increases for competitors of a sexual species, and hence, they should also be sexual. In this way sexual reproduction is a self-maintaining trait as long as biological interactions play a prominent role. *Mutatis mutandis*, in biotopes where that role is less effective, due to harsh conditions (high altitudes and latitudes, xeric biotopes), or to isolation

(islands), asexual reproduction is favoured. In such places, when population density is comparatively low and mate-finding thus may be difficult, thelytoky has an additional advantage (Gerritsen 1980). Often asexually reproducing species are polyploid, which is considered to have extra adaptive value, especially under harsh conditions (e.g. Suomalainen 1962). Polyploidy is predominantly associated with apomictic thelytoky. Two tactics were defined for thelytokous species (IX and X), one (IX) contains species with seasonal iteroparity and thelytoky. Seasonal iteroparity is seen as a trait to overcome years of low reproduction. Murdoch (1966) showed that in the carabid beetle *Agonum fuliginosum* there was an inverse relationship between reproduction and survival: individuals which could not reproduce, or hardly reproduced, due to unfavourable conditions, had a better chance of survival and reproduction in the next season. In species with both thelytokous and sexual forms (geographic parthenogenesis, Suomalainen, 1950), a continuum can be expected. In automictic thelytoky, indications of the existence of intermediates are present in the form of atavic males (Taberly 1988). These genuine males produce a few spermatophores but do not seem to play a role in reproduction, because the thelytokous females do not pick up the spermatophores. A trend in sexually reproducing species is given by Trivers & Willard (1973) stating that food shortage or other environmental stress might select for the production of female offspring. Selection for the production of either males or females is shown by Starzyk & Witkowski (1986) in cerambycid beetles. Thus, thelytoky in harsh environments can be either automictic, the end of a, possibly continuous, shift in sex-ratio, or apomictic, with polyploidy very probable. This results in two ways of maintaining some genetic variation without mating. In sexual species, the effect of a female-biased sex-ratio due to harsh environmental conditions may be equivalent to that of automictic thelytoky. Seasonal iteroparity is also associated with species living under harsh conditions.

Other traits form a more distinct continuum. Diapause in its obligate form can be seen as the adaptational end of a continuum that runs from quiescence via facultative diapause. The continuum of phoresy, running from accidental, via facultative, either to obligate carrier-unspecific phoresy (with or without special adaptations), or to obligate carrier-specific phoresy finally ends in parasitism, as pointed out in the section on obligate and facultative phoresy and carrier-specificity.

Borderline species may give rise to some difficulties in the practical use of the system of life-history tactics, which is a general problem of classification. Although all classifications have their borderline cases, it may be concluded that the present classification of life-history tactics of microarthropods is based on well-defined, determinable life-history traits. The defined tactics and the component life-history traits may be applicable for other higher taxa than microarthropods.

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Microarthropod communities

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3

Applications of microarthropod life-history tactics in

nature management and ecotoxicology

SUMMARY. The practical use of microarthropod life-history tactics in nature management and ecotoxicology is demonstrated. A key to the tactics is presented to facilitate the use of the life-history tactics. Examples are given of the distribution over these tactics of microarthropods from a forest, a grassland, and a salt marsh. The process of decomposition of grass leaves in litterbags is illustrated using life-history tactic diagrams. Effects of various disturbances can be well documented by shifts in the distribution of life-history tactics of species. Irregular unpredictable disturbances lead to an increased representation of phoresy tactics. Regular disturbances lead to an increased representation of synchronization tactics. Permanent and persistent pollution, finally, leads to an increased representation of tactics with thelytokous reproduction. The consequences of the latter for ecotoxicology are discussed. It is concluded that microarthropod life-history tactics meet the formerly described criteria permitting comparisons between effects of management measures and pollution in different biotopes and countries.

INTRODUCTION

In Chapter 2 I followed Stearns (1976) in defining life-history tactics as co-adapted sets of meaningful life-history traits. A classification of tactics was primarily based on properties of microarthropods, but the composing traits are general and widespread in all kinds of organisms. This classification is also supposed to have a more general value and it is more differentiated than previous ones (MacArthur & Wilson 1967; Grime 1977, 1979; Southwood 1977, 1988; Stearns 1976; Holm 1988).

The objective of this chapter is to apply this classification in ecotoxicology and nature management. An identification key is presented to improve the accessibility of the life-history tactics of microarthropods.

Several examples are presented to illustrate that the system of life-history tactics meets the advantages *sensu* Grime *et al.* (1988): allowing comparisons between biotopes, countries and effects of different environmental impacts.

Six hypotheses embracing all three major groups of life-history tactics, i.e. reproduction tactics, synchronization tactics, and dispersal tactics (Chapter 2), are tested.

(1) In relatively undisturbed ecosystems specialized tactics are uncommon among microarthropods.

(2) During the process of decomposition of *Avenella* leaves in litterbags, initially an increase of fast colonizers (dispersal tactics) is expected, whereas in later stages species adapted to more constant environments may take over (tactics with thelytoky).

In disturbed ecosystems, (3) such as cattle-grazed (a small-amplitude irregular disturbance) versus ungrazed grasslands, and (4) such as high-production grasslands with intensive management (a high-amplitude irregular disturbance) versus semi-natural grasslands, a comparatively higher fraction of dispersal tactics and a lower fraction of tactics with thelytoky is expected in the disturbed grasslands.

(5) In situations with a more regular disturbance, such as the fluctuation of the waterlevel in a storage reservoir affecting the mite fauna on annually drained flood plains, a relative increase of synchronization tactics is expected. With increasing depth in such a storage reservoir uncertainty about submergence increases and only species best adapted to such conditions reach high densities.

(6) In biotopes with a persistent pollution by heavy metals or persistent insecticides, the constancy of this pollution may lead to an increase of microarthropod life-history tactics with thelytoky. Next to predictable, such a biotope has become a harsh environment, where species interactions presumably play a minor role, so sexual reproduction may be less favoured (Glesener and Tilman 1978, Chapter 2).

MATERIALS AND METHODS

Allocation of a species to a life-history tactic is done using the key in Appendix 3.1. Datasets of microarthropods used are partly from literature, partly from own material (Siepel 1990). Only datasets on microarthropods identified to the species level were used, because in orders, families and even genera several tactics can occur. Furthermore, datasets should preferably not be limited to one order of microarthropods only, because not all tactics occur in each order.

For the dominant species in the datasets references will be given to support the identification of their life-history tactics. A species is called dominant when its number exceeds 5% of the total number of microarthropods in the sample. If data for a species are missing, the predominant life-history traits in soil microarthropods are presumed: sexual reproduction, iteroparous oviposition, no phoresy and no synchronization, resulting in tactic XI. Therefore, no conclusions can be drawn on changes in this tactic. All conclusions will be based on positively identified tactics.

RESULTS

Relatively undisturbed ecosystems

The distribution of the microarthropods (Acari and Collembola) among life-history tactics is presented for a forest soil using data of Van de Bund and Eijsackers (1986), a grassland soil using data of Siepel and Van de Bund (1988) ("Bovenbuurt B") and a salt marsh using data of Luxton (1967) ("Puccinellietum series") (Table 3.1).

The dominant species of the forest soil were: Platynothrus peltifer (C.L. Koch 1844), a long-living thelytokous species (Taberly 1987): tactic IX; Tectocephus velatus (Michael 1880) and Oppiella nova (Oudemans 1902), both iteroparous thelytokous species (Grandjean 1941; Wooding & Cook 1962): tactic X; Atropacarus striculus (C.L. Koch 1836) an iteroparous sexually reproducing species: tactic XI. None of these oribatid species is known to be phoretic or to have a diapause, which also holds for the sexually reproducing mesostigmatid mite Pergamasus vagabundus Karg 1968 (Karg 1971): tactic XI.

The dominant species in the grassland soil are: Microppia minus (Paoli 1908), a thelytokously reproducing short-living species (Luxton 1981; Taberly 1987): tactic X; Brachychthonius bimaculatus Willmann 1936 and Sellnickochthonius immaculatus (Forsslund 1942), species assumed to be sexually reproducing by analogy to the related Eobrachychthonius oudemansi Van der Hammen 1952 (West 1982): tactic XI. The listed oribatid mites do not have a diapause or phoretic behaviour, which also holds for the sexually reproducing collembolan Folsomia quadrioculata (Tullberg 1871) (Gregoire-Wibo 1974): tactic XI.

The dominant species of the salt marsh are the oribatids Punctoribates quadrivertex (Halbert 1920) and Hygroribates schneideri (Oudemans 1905), both sexually reproducing species (Luxton 1966): tactic XI. The sexually reproducing mesostigmatid mite Halolaelaps nodosus Willmann 1952 (Karg 1971) and the actinedid species Cheylostigmaeus scutatus (Halbert) have a facultative egg resting stage the latter by analogy to the related C. pannonicus (Willmann) (Tamm 1984): tactic VIII.

Microarthropod communities

Table 3.1. Percentages of individuals per life-history tactic of the microarthropod community of a forest soil, a grassland soil and a salt marsh zone; n is the total number of individuals, s the total number of species observed.

Life history tactic	Forest soil	Grassland soil	Salt marsh zone
I	0	0	0
II	1.99	3.04	7.55
III	0.83	0.78	4.01
IV	0.03	0.37	0
V	0.21	3.23	2.39
VI	0	0	0
VII	0	0.02	0
VIII	0	0	7.42
IX	7.94	0	0
X	15.40	11.95	0
XI	71.87	80.60	78.62
XII	1.53	0.02	0
n	3863	6185	2966
s	72	93	20

The salt marsh compared to both the forest and the grassland soil has no representatives with a thelytokous reproduction (tactics IX and X), but has representatives of tactic VIII, facultative diapause or quiescence. The grassland soil compared to the forest soil lacks long-living thelytokous species (tactic IX), and scores a little higher on the fraction of facultative phoretic species. These data suggest increasing environmental dynamics in the sequence forest soil - grassland soil - salt marsh zone. The results are consistent with the first hypothesis: specialized tactics are relatively uncommon in undisturbed ecosystems, although the fractions of dispersal (II, III, IV) and synchronization tactics (V, VI, VII, VIII) in the salt marsh may be underestimated, because little life-history information exists on the majority of the salt marsh species.

Changes during decomposition in litterbags

The life-history tactics of microarthropods occurring during the decomposition of leaves of the grass *Avenella flexuosa* (L.) Dreyer in litterbags placed between litter and mineral soil are presented in Figure 3.1. Data concern a total of 17,695 individuals (eight sampling dates and initial soil microarthropod community together) and 135 species (Siepel, 1990).

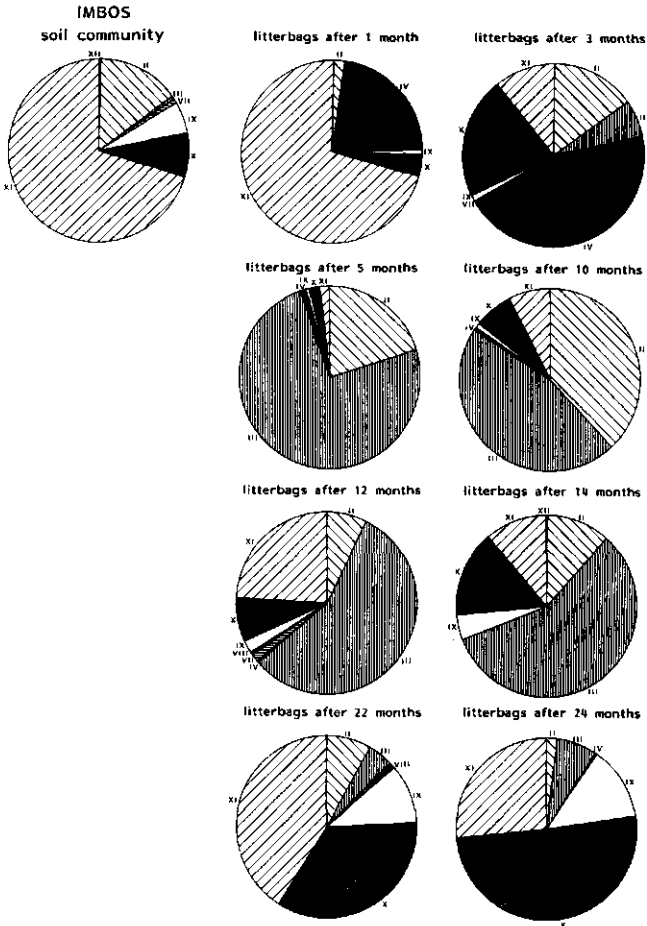


Figure 3.1. Life-history tactics of microarthropods (mites and spring-tails) during decomposition of leaves of *Avenella flexuosa* in litterbags placed between litter and mineral soil. Data from Siepel (1990).

Microarthropod communities

Dominant species in any of the sampling periods were: the collembolans Hypogastrura denticulata Bagnall 1941, a relatively short-living sexually reproducing species (Hale 1965): tactic XI; Onychiurus furcifer (Börner 1901) a sexually reproducing species (Hale 1965): tactic XI and Onychiurus s-vontoernei (Gisin 1957), assumed to have sexual reproduction; tactic XI. In the genus Onychiurus both sexual (O. tricampatus Gisin 1956; Hale 1964) and thelytokous reproduction (O. armatus (Tullberg 1869); Grégoire-Wibo & Snider (1983) and O. procampatus Gisin 1956; Hale 1964) occur, in unknown cases therefore species were assumed to be sexually reproducing. Isotomiella minor (Schäffer 1896) is thelytokously reproducing (Petersen 1980): tactic X. The same holds for Tullbergia krausbaueri (Börner 1901) according to Petersen (1971): tactic X. The listed Collembola are not phoretic nor do they have a diapause. Two species of tarsonemids were found to be dominant. Scutacarus quadrangulus Paoli 1911 and Pygmephorus cf. haarioevi. Members of the Scutacaridae as well as the Pygmephoridae were phoretics (Binns 1982; Desender & Vanechoutte 1984; Lindquist 1986), which is assumed to be facultative for both species: tactic II. The astigmatid mites Schwiebia talpa Oudemans 1916 and Schwiebia lebruni Fain 1977 are known to be phoretic as hypopi and to be carrier-unspecific (Karg 1987): tactic III. The mesostigmatid Peramesus truncus Schweizer 1961 is not phoretic and sexually reproducing (Karg 1971): tactic XI; Alliphus siculus (Oudemans 1905) is phoretic in all life stages (Karg 1971): tactic IV and Uropoda minima (Berlese 1910) is phoretic (Athias-Binche 1984) and thelytokously reproducing (Athias-Binche 1981): tactic II. For the oribatid mite Sellnickochthonius zelawaiensis (Sellnick 1928) the same tactic was assumed as for the congeneric S. immaculatus before: tactic XI. Nothrus silvestris (Nicolet 1855) has a thelytokous reproduction (Grandjean 1941) and is long-living (Sengbush 1958): tactic IX. Mediopopia subpectinata (Oudemans 1900) has sexual reproduction and lives relatively short (Luxton 1981): tactic XI.

Compared to the initial soil microarthropod community more obligate phoretics (tactics III and IV) were observed in the early stages of decomposition. Species phoretic in any life stage (tactic IV) occurred for a very short period of time; this was the most 'r-selected' tactic recognized (Chapter 2). Somewhat later facultative phoretics (tactic II) increased.

During the later stages of decomposition species with thelytokous reproduction (tactics IX and X) increased. So the initial abundant growth of fungi and bacteria was exploited by phoretic species, obligate phoretics rather than facultative phoretics (fungivores, bacteriovores as well as (nematode) predators). These species were replaced in later stages of decomposition, when fungal growth is less abundant, by microarthropods adapted to a rather constant environment. The majority of the species in that stage of decomposition in the litterbags had a thelytokous reproduction. The final stage of decomposition did not resemble the initial soil community (Fig. 3.1), because of the location of the litterbags in the stratum between litter and mineral soil. Faunal composition of the final stage resembled the euedaphic faunal community.

These results are consistent with the second hypothesis: an initial increase of fast colonizers (phoretics) and a relative large fraction of thelytokous species in the late stages of the decomposition process.

The effects of fertilization and cattle grazing

Siepel and Van de Bund (1988) investigated the microarthropod community of three types of grasslands: unfertilized, little and heavily fertilized. In each type, cattle-grazed and mown grasslands were represented. The data showed a shift in life-history tactics from unfertilized to heavily fertilized grasslands and a difference between mown and cattle-grazed grasslands.

Dominant species among the Oribatida in any of the grasslands were *Brachychthonius bimaculatus* and *Selnickochthonius immaculatus*: tactic XI; *Microppia minus* and *Tectocepheus velatus*: tactic X as pointed out above. *Liebstadia similis* (Michael 1888), *Minunthozetes semirufus* (C.L. Koch 1841), *Ramusella clavipectinata* (Michael 1885) and *Achipteria coleoptrata* (Linnaeus 1758): tactic XI (Luxton 1981; Sengbush 1958). Dominant Collembola were: *Hypogastrura denticulata* tactic XI as pointed out above and *Friesea mirabilis* (Tullberg 1871), *Isotoma sensibilibis* (Tullberg 1871), *I. viridis* (Bourlet 1839), *I. olivacea* (Tullberg 1871) and *Proisotoma minuta* (Tullberg 1871): tactic XI (sexual reproduction) (Hale 1965), and finally *Sminthurinus aureus* (Lubbock 1862): tactic VIII (with a facultative diapause: Van Straalen et al., 1985). Dominant Tarsonemida were: *Scutacarus quadrangulus*: tactic II as pointed out above, and *Pygmephorus mesembrinae* (Canestrini 1881): tactic II, facultative phoresy (Krczal 1959). The only dominant mesostigmatid mite was *Dendrolaelaps rectus* Karg 1962, which is facultatively phoretic (Karg 1971): tactic II.

In cattle-grazed compared to ungrazed grasslands, facultative phoretics (tactic II) and obligate phoretics (tactics III and IV) were more abundant (Wilcoxon two-sample test: $p < 0.025$). Figure 3.2 gives pie diagrams of the life-history tactics found in an ungrazed and a cattle-grazed grassland. The result is consistent with the third hypothesis: a comparatively larger fraction of species with dispersal tactics and a lower fraction of species with thelytoky in the cattle-grazed grasslands.

In fertilized grasslands obligate phoretics (tactics III and IV), and species with facultative diapause or quiescence (tactic VIII) were more abundant than in unfertilized grasslands, while in unfertilized grasslands thelytokously reproducing species with or without seasonal iteroparity (tactics IX and X, respectively) were more abundant (Wilcoxon test: $p < 0.01$). Figure 3.3 presents the life-history tactics in an unfertilized and a heavily fertilized grassland. As expected from the fourth hypothesis the heavily fertilized grassland had a higher fraction of species with dispersal tactics and a lower fraction of species with thelytokous reproduction. The differences in this high-amplitude disturbance were more pronounced than in the small-amplitude disturbance of cattle-grazing.

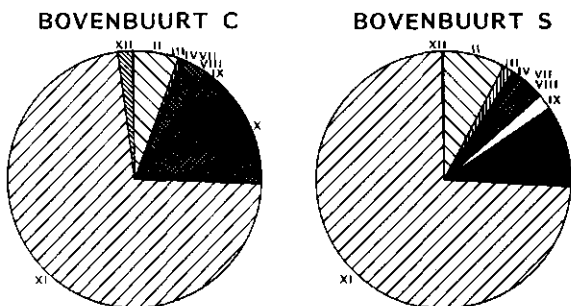


Figure 3.2. Life-history tactics of microarthropods (mites and spring-tails) from a mown (Bovenbuurt C) and a cattle-grazed grassland (Bovenbuurt S) in The Netherlands. Data from Siepel & Van de Bund (1988).

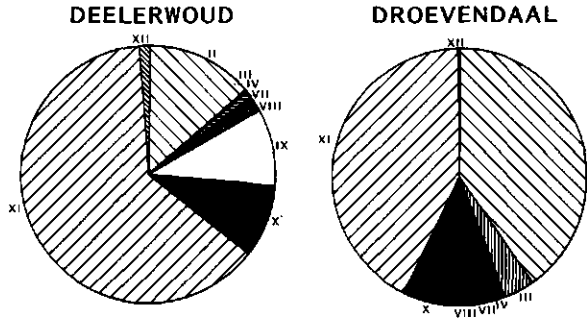


Figure 3.3. Life-history tactics of microarthropods (mites and springtails) from an unfertilized (Deelerwoud) and a highly fertilized grassland (Droevendaal: 400 kg N ha⁻¹yr⁻¹) in The Netherlands. Data from Siepel & Van de Bund (1988).



Figure 3.4. Proportion of mites with life-history tactic VIII (facultative diapause or quiescence) plotted against the depth in meters beneath a completely filled storage reservoir in Germany. Data from Tamm et al. (1984).

Both fertilization and cattle-grazing led to a microarthropod community more adapted to disturbance. The species occurring are able to flee either in space (phoretics) or in time (diapause). Predictability of the environment decreased which can be concluded from the lower fraction of thelytokously reproducing species compared to sexually reproducing species.

The microarthropod community of an annually drained flood plain

Data on the mites of an annually drained flood plain are provided by Tamm *et al.* (1984).

The dominant actinidid species *Neomolgus obsoletus* (Berlese) and *Cheylostigmaeus pannonicus* Willmann have the possibility of long submergence in the egg stage (Tamm 1984): tactic VIII.

In Figure 3.4 the proportion of life-history tactic VIII (facultative diapause or quiescence) is plotted against the depth in the storage reservoir beneath maximal water level (completely filled reservoir). The more under the maximum level, the more unpredictable the environment becomes in terms of chance of submergence. The increase of the proportion of life-history tactic VIII with increasing depth is significant (F-test: $p < 0.05$). Consistent with the fifth hypothesis an increase of the fraction of microarthropods having facultative diapause or quiescence (tactic VIII) with increased chance of submergence was found. This clearly illustrates the unpredictability in time of such a biotope.

The effect of persistent pollutants

Pollution with heavy metals and persistent pesticides may substantially alter the microarthropod community in the long run. The following studies with data on microarthropods, (almost) all identified to the species level, allow evaluation of pollution effects over a long period of time.

Heavy metal pollution

Data on species composition of Collembola in a transect up to 20 km away from a brass mill were presented by Bengtsson and Rundgren (1988). Presumably because of their different soil types, three of their eight sample sites (XI, IV and VI) had a significantly lower pH(H₂O) (F-test: $p = 0.025$), a lower CEC (F-test: $p < 0.001$), and a lower Ca content (F-test: $p < 0.001$) as calculated from their table 1. These sites were excluded from the present analysis.

The dominant species were: *Willemia aspinata* Stach 1949, *W. anophthalma* Börner 1901, *Onychiurus asoloni* (Börner 1901), *O. armatus* (Tullberg 1869), *Tullbergia callipygos* Börner 1902, *T. sylvatica* Rusek 1978, *T. tenuisensillata* (Rusek 1978), *T. italica/yossi*, *T. macrochaeta* (Rusek 1978), *Folsomia fimetarioides* (Axelson 1905), *F. candida* (Willem 1902), *Isotomiella minor* (Schäffer 1876) and *Isotoma notabilis* (Schäffer 1896), all of them having a thelytokous reproduction and a relatively short lifetime: tactic X (Petersen 1971, 1980; Gregoire-Wibo & Snider 1984; Van Straalen *et al.* 1985). Dominant species having sexual reproduction (tactic XI) were: *Eriosea mirabilis* (Tullberg 1871), *Anurida pygmaea*

Microarthropod communities

(Bärner 1901), *Folsomia quadrioculata* and *Lepidocyrtus lanuginosus* (Gmelin 1788) (Gregoire-Wibo 1974; Hale 1965).

Figure 3.5 presents the percentage of occurrence of thelytokously reproducing collembolans (tactic X) at the five remaining sites in the transect from the brass mill. The decrease in tactic X with increasing distance from the brass mill was significant (F-test: $p < 0.05$). The most polluted sites mainly had *Collembola* with a thelytokous reproduction.

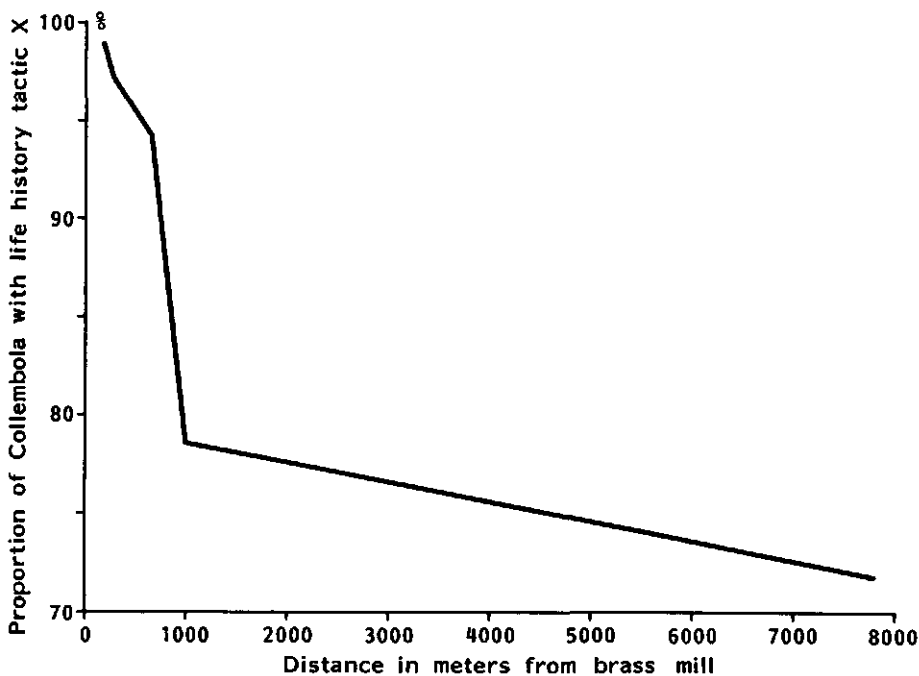


Figure 3.5. Proportion of *Collembola* with life-history tactic X (thelytokous reproduction and relatively short lifetime) plotted against the distance (in meters) from a brass mill in Gusum (Sweden). Data from Bengtsson & Rundgren (1988).

Table 3.2. Percentages of individuals per life-history tactic of the microarthropods in a forest soil: A=control plot, C=50 kg H₂SO₄ ha⁻¹ and D=150 kg H₂SO₄ ha⁻¹ applied annually. Based on Bååth et al. (1982).

Life-history tactic	A	C	D
II	0.03	0.25	0.04
III	6.85	5.99	6.30
V	0.14	0.09	0.15
IX	0.99	0.83	2.58
X	24.99	37.61	47.13
XI	66.77	54.79	43.69
XII	0.22	0.43	0.11

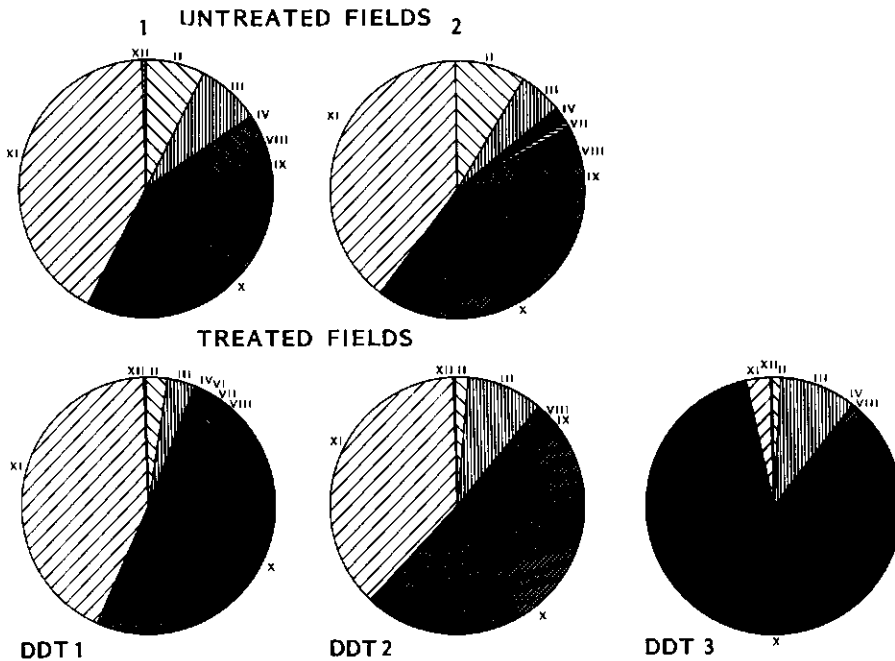


Figure 3.6. Life-history tactics of microarthropods (mites and spring-tails), sampled in 1986, in a long-term DDT application experiment in Wageningen (The Netherlands). Two plots received no DDT (untreated); DDT1 received 300 mg.m⁻²y⁻¹, DDT2 600 mg.m⁻²yr, and DDT3 2000 mg.m⁻²yr⁻¹ from 1953-1968. Data from Van de Bund (unpublished).

Microarthropod communities

Experimental acidification

The data of Bååth *et al.* (1982) concern both Collembola and Acari sampled in 1976 after six years of artificial application of acid rain.

The dominant species at their sites are: "Brachychthoniidae", sexual reproduction is assumed here for all members of the family although confirmed for only one (West 1982): tactic XI; the same tactic is given for Nanorchestes arboriger (Berlese), Tectocephus velatus, Oppiella nova and Tullbergia krausbaueri have thelytokous reproduction (tactic X) and Schwiebia spec. are facultative phoretics (tactic II).

Table 3.2 lists the percentages of the life-history tactics present. The observed increase in thelytokously reproducing microarthropods (tactic X) was almost significant $p=0.06$ (F-test). Hence, artificial acidification seems to lead to an increase in the proportion of thelytokously reproducing species already after six years.

Persistent pesticides

Long-term effects of DDT have been studied by Van de Bund (1965, 1976). In 1986 he sampled the microarthropod fauna of the same plots again and found the remnants of DDT and derivatives about 30% of the total amount supplied (Van de Bund, unpublished, Martijn *et al.* 1993). Figure 3.6 presents life-history tactics of microarthropods in two untreated plots (no DDT applied) and three treated plots in 1986.

Dominant species in the plots were: Tullbergia krausbaueri, Isotoma notabilis, Microppia minus, Oppiella nova and Tectocephus velatus, all thelytokously reproducing species (tactic X), and Cosmolaelaps claviger (Berlese 1883) and Arctoseius cetratus (Sellnick 1940) phoretic as adults (Afifi & Van der Geest 1984; Binns 1974): tactic IV.

The obvious increase of the proportion of thelytokously reproducing microarthropods is significant (F-test $p<0.05$). The addition of a persistent pesticide to the soil apparently made the environment more suitable for thelytokously reproducing than for sexually reproducing species, which is consistent with hypothesis 6.

DISCUSSION

Both in heavy metal polluted and in persistent pesticide polluted areas the proportion of thelytokously reproducing microarthropods increased. In Chapter 2 it was pointed out that thelytoky is favoured in constant rather than in variable biotopes. It seems that the presence of a very dominating environmental factor, which is constantly present, has the same effect. The clone(s) of the thelytokous species, present at those sites and resistant to the pollutant, or able to avoid it, may reproduce more effectively than other clones and than sexually reproducing species. In the sexually repro-

ducing species an well-adapted genotype may be disrupted every time in reproduction. The proportion of thelytokously reproducing microarthropods to their total number may be a good indicator of persistent pollutants, apparently of any kind.

Such a thelytokously reproducing population of microarthropods cannot be considered 'adapted' to the changed environment. Part of the initial population (one or a few clones) may by chance be resistant to the pollutant or able to avoid it. So, the genetic variability in the initial (before pollution) population, or in reference populations in unpolluted areas is expected to be much higher than in the population in the polluted environment. Such an effect is in contrast with the effect of intermediate (ir)regular disturbances which result in a high clonal diversity according to Sebens and Thorne (1985).

The common use of thelytokous species in laboratory experiments to evaluate the toxicity of pollutants and to extrapolate the outcome to species assemblages is open to criticism. Ironically, many laboratory experiments on this subject are carried out with thelytokously reproducing species: in microarthropods e.g. *Folsomia candida* by Butcher and Snider (1975) and Thirumurthi and Lebrun (1977); *Onychiurus armatus* by Bengtsson *et al.* (1983a, 1985a, 1985b), *Platynothrus peltifer* by Streit (1984) and Van Straalen *et al.* (1989); and in earthworms e.g. *Eisenia foetida* (parthenogenetic according to Gavrilov 1960, but see Van Gestel 1991) by Hartenstein *et al.* (1981); *Dendrobaena rubida* (partly parthenogenetic according to Evans and Guild, 1948) by Bengtsson *et al.* (1983b, 1986) and *Octolasion cyaneum* by Streit and Jaeggy (1983) and Streit (1984). Thelytokous species, especially when sampled from a polluted environment, can be expected to yield biased toxicity test results, a risk which would be less in sexually reproducing species. The list of conditions for a representative soil organism to study ecotoxicological effects given by Bengtsson *et al.* (1983b) has to be extended with: 'the species must have sexual reproduction'.

From the results presented in this paper it should be obvious that, based on the life-history tactics of species it is possible to make comparisons of the impact of management measures in different biotopes (forest, grassland, annually drained flood plains) and the effect of pollution (DDT, heavy metals, acidification) in different areas (Germany, The Netherlands, Sweden) on the soil microarthropod community. So, it seems likely that the system of life-history tactics can be applied in various areas of practical importance.

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Microarthropod communities

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Microarthropod communities

Appendix 3.1. Key to the life-history tactics of microarthropods.

- 1 - the species is phoretic, either obligately or facultatively,
not just accidentally 2
- the species is not phoretic or just accidentally phoretic 6
- 2 - the species feeds on the host/carrier as an important food
source in one or all life stages attached to the
host/carrier 3
- the species does not feed on the carrier, or the carrier can
at least not be considered an important food source in any
life stage attached to the carrier 4
- 3 - the species is free-living part of its life cycle **Tactic Ib**
- the species spends its entire life cycle on the host **Tactic Ia**
- 4 - the species is either facultatively phoretic, or obligately
phoretic but in the latter case with a comparatively low
development rate, or a low egg production; all types of
reproduction possible **Tactic II**
- the species is obligately phoretic, has a fast development
rate and relatively high egg production; sexual or arrhenotokous
reproduction only 5
- 5 - juvenile stages of the species are phoretic only, often
specially adapted for phoretic transport **Tactic III**
- the species is phoretic in any stage including adults **Tactic IV**
- 6 - the species has an obligate or facultative diapause in its
life cycle, or synchronization of its life cycle by quiescence
during some period(s) 7
- the species has continuous generations in which development can
be slow in some periods, which is not considered a quiescence 10
- 7 - the species has an obligate diapause or obligate aestivation,
or alternate generations have one of these **Tactic V**
- the species has a facultative diapause or quiescence 8
- 8 - the species has an anemochorous dispersal **Tactic VII**
- the dispersal of the species is not predominantly anemochorous 9
- 9 - the species has a semelparous oviposition **Tactic VI**
- the species has an iteroparous oviposition **Tactic VIII**
- 10 - the species has a thelytokous reproduction 11
- the species has a sexual reproduction 12
- 11 - the species is relatively short living **Tactic X**
- the species is relatively long living **Tactic IX**
- 12 - the species has an iteroparous oviposition **Tactic XI**
- the species has a seasonal iteroparous oviposition **Tactic XII**

Feeding guilds of oribatid mites

based on their carbohydrase activities

SUMMARY. Carbohydrase activity was analysed in 49 species of oribatid mites and one acaridid mite sampled from natural populations. Enzyme activity was determined for the main differentiating food components: cellulose, a component of cell-walls of green plants; chitin, a component of fungal cell-walls; and trehalose, a component of fungal cell-contents. Feeding guilds were defined based on the activity of the three carbohydrases. The nomenclature of the feeding guilds was adopted from that of ruminants. Five major feeding guilds were distinguished: herbivorous grazers (9 species), fungivorous grazers (8), herbo-fungivorous grazers (16), fungivorous browsers (7) and opportunistic herbo-fungivores (8) and two minor guilds in oribatids: herbivorous browsers (1) and omnivores (1). The feeding guilds presented are operationally better defined in terms of resource exploitation than the macro-, micro- and panphytophages used hitherto.

INTRODUCTION

Feeding guilds of phytophagous oribatid mites have been defined by Schuster (1956), and refined by Luxton (1972) and various authors since (e.g. Kaneko, 1988; Wallwork, 1983). The classification of feeding types in guilds is important to understand the role a species plays in its biotope. Their function in the decomposer community might be comminution of organic matter, alteration of microbial activity or dispersal of decomposer micro-organisms (Wallwork, 1983; Swift et al., 1979; Behan and Hill, 1978), and some species may be ground-dwelling herbivores without any function in decomposition. The current classification into three phytophagous guilds i.e. macrophytophages (feeding on higher plant

material, either wood or leaf), microphytophages (feeding strictly on the microflora) and panphytophages (feeding on all kinds of plant or fungal tissues) is based primarily on the function oribatid mites were thought to have: fragmentation of litter. It has become clear that oribatids may also have an influence on decomposition through grazing on fungi and bacteria (Van der Drift and Jansen, 1977; Hanlon, 1981; Hanlon and Anderson, 1979). The present descriptions of feeding guilds are not specific enough with respect to this influence on decomposition. Microphytophages for instance may feed on bacteria or fungi (and influence decomposition), or on algae (without decomposer function), or any combination of those (Luxton, 1972); so it is not easy to relate this guild to any specific decomposer function.

For a reliable relationship between the possible function of species in the decomposer community and the feeding guild the latter must be defined as strictly and uniquely as possible. Hofmann and Stewart (1972) classified East African ruminants into two major groups: roughage eaters or grazers having a subdivided, capacious rumen with uneven papillation; and concentrate selectors or browsers having a relatively small rumen adapted to a fast turnover of food. Between these two groups an intermediate group was distinguished. Our nomenclature of feeding guilds of oribatid mites is similar to this classification in the use of the terms: grazer and browser. Grazers have the ability to digest both cell-walls and cell-contents; browsers are only able to digest cell-contents. In our study feeding guilds are based on the capabilities of oribatid mites to digest plant or fungal tissues, i.e. cellulose, a major component of green plant cell-walls; chitin, a major component of fungal cell-walls; and trehalose, a component of fungal cell-contents (the combination of both chitin and trehalose is probably unique for fungi, Hegnauer, 1962). Trehalose is also found in lichens (Darnley Gibbs, 1974), in Cyanophytae, to some extent in Rhodophyta and in Selaginellaceae (Hegnauer, 1962), and in Myxophyta (Hegnauer, 1986). In exceptional cases it has been found in reasonable amounts in higher plants (Hegnauer, 1963). Darnley Gibbs (1974) reported it from higher plants under environmental stress, especially drought. In our study the digestive capabilities of mites were measured by their cellulase, chitinase and trehalase activity in field populations.

It was not our aim to define exactly which compounds a mite can digest. The three enzymes mentioned were selected to yield the best differentiation in terms of feeding guilds. Carbohydrase activity on a qualitative basis has been studied before in oribatid mites by Luxton (1972, 1979) and Zinkler (1970) who made also some quantitative measurements. Maybe other groups of gut enzymes, e.g. esterases and proteases in future can also be used to differentiate between feeding patterns if

these enzymes act on foodtype specific components. In our study activity measurements of the three carbohydrases were carried out quantitatively.

MATERIALS AND METHODS

Analyses of carbohydrase activity were carried out in mites sampled from natural populations, to prevent drawing conclusions on enzyme activities which might be induced in populations reared in the laboratory. From May until November 1989 living mites were sampled from various biotopes: soil, litter, moss (both on trees and on solid surfaces), lichens, herbage, trees and sphagnum pools. For analysis of the activity of three carbohydrases (cellulase, chitinase and trehalase) 49 of the most common species of oribatid mites and one species of acaridid mite were selected; the oribatid mite species chosen were selected as far as possible from the different families according to Balogh (1972) and Marshall et al. (1987). The acaridid mite was added to the list because it was thought to represent a feeding guild (a browser) which might be not common among oribatids.

To identify the species when alive a rather laborious method had to be followed. Species were extracted from substrate and prepared for microscopic inspection as described by Siepel and Van de Bund (1988). When one of the oribatid mite species was numerous in the substrate and no confusion could arise with any other species, that substrate was sampled for living mites of that species. If no species in that substrate could be sampled alive without confusion with other species, a substrate was sampled elsewhere and the procedure started again. It is because of this procedure that no members of Brachychthoniidae and Suctobelbidae and only one member of Oppiidae (*Ramusella clavipectinata*) were included in this study. In these families many species were regularly present together which impeded a reliable identification of the mites to be analysed. Four replicate samples were obtained at different sampling dates and different localities.

The substrates soil, litter, moss, lichens, and sphagnum were sampled and placed in a Tullgren funnel to collect the mites in water. Herbage and trees were sampled using a sweep net; these samples were put in water and the mites were removed by hand sorting. The live mites were counted and about 250 μg mite fresh mass was put in one glass tube per enzyme analysis. The number of mites per analysis varied from 1 (also when the mite weighed more than 250 μg) up to 90 specimens. In the analyses of carbohydrase activity in *Licneremaeus licnophorus* 80 specimens

were used which corresponded to about 100 μ g. The mites were pulverized just before the incubation.

Activity of cellulase (β 1-4 glucan-glucano-hydrolase, EC 3.2.1.4) was determined by colorimetrically measuring the amount of glucose at 444 nm after colouring with Sigma method no 510 (1 capsule in 50 ml water and 1.6 ml colour reagents) during 45 min at room temperature. Glucose is the product of animal cellulase activity after 4 h in a 1% carboxymethylcellulose Sigma C-8758 at pH = 5.0 (created by addition of phosphoric acid) and 37°C (Siepel, 1990).

Activity of chitinase (poly β -1,4-(2-acetamido-2-deoxy)-D-glucoside glycano hydrolase, EC 3.2.1.14) was determined by colorimetrically measuring the amount of acetyl-glucosamine at 585 nm after boiling for 10 min, dissolving 100 ml 0.8 M $K_2B_4O_7$ in 0.5 ml reagents, again boiling for 3 min, and adding 1 g p-dimethyl benzaldehyde in 100 ml 98% acetic acid with 1.2% 12N HCL (Jeuniaux, 1966). Acetyl-glucosamine is the product of animal chitinase activity after 4 h in a 0.5% suspension of chitin (Sigma C-3641) at pH = 5.1 (created by 0.6M citric acid and 1.2M bisodium hydrogen phosphate) and 37°C (Siepel, 1990).

Activity of trehalase (α , α' -glucoside 1-glucohydrolase, EC 3.2.1.28) is determined by measuring the amount of glucose as described above under cellulase activity assay. Glucose is the product of animal trehalase activity after 4 h in a 1% trehalose solution (α ,D-glucopyranosyl- α ,D-glucopyranoside) Sigma T-5251 at pH 5.7 (created by addition of phosphoric acid) and 37°C (Siepel, 1990).

For every carbohydrase activity measurement (cellulose, chitinase or trehalase) four replicate samples were analysed. In addition to the samples for analysis of carbohydrase activity blanks samples were also prepared. The procedure for these blanks was the same except for the omission of the incubation period at 37°C.

RESULTS

In Table 4.1 carbohydrase activities are presented for the mite species investigated, ranked per feeding guild. When a blank result did not differ significantly from the mean of the incubated samples, it was concluded that the activity of the enzyme was negligible; this concerned low values only.

Based on the carbohydrase activities the oribatid mites were classified into five major guilds and two small ones with one species each as mentioned in Table 4.1. The feeding guilds will now pass in review.

Herbivorous grazers: have cellulase activity only, feed on green plants (including algae) and are able to feed on both the cell-contents and the cell-walls. The nine species in this guild can feed on living plants as well as on litter and are in that case important as comminutors in the decomposer community. A comparatively low cellulase activity suggests either a low metabolic rate or a transition towards the next feeding guild.

Herbivorous browsers: defined by the absence of activity of the three enzymes analysed. This may well apply for most predators, carrion feeders and bacteria feeders, too. Feeding experiments must differentiate here. The only species in this "guild" is *Melanozetes mollicomus*, which might be a carrion feeder just like the related *Fuscozetes fuscipes* (Wallwork, 1958).

Fungivorous grazers: have chitinase activity as well as trehalase activity. The eight species in this guild feed on fungi, and are able to digest both cell-walls and contents. Of course these species, because of their chitinase activity can also feed on dead mycelium, something the next guild is unable to. Species with relatively low chitinase activity (compared with other species and with their trehalase activity) may be transitional cases to the next guild. Species having both lower chitinase and trehalase activity may be metabolically less active.

Fungivorous browsers: are able to digest trehalose only. The only acarid mite investigated belongs to this guild, as expected. Unexpected was the presence of a rather large number of oribatids. The lower trehalase activities of some species probably do not indicate lower metabolic rates, which seems rather unlikely here because of the active mode of behaviour of these species. A transition, however, towards the group of herbivorous browsers is quite probable, especially when it is noted that these species might be lichenivorous browsers, because trehalose also occurs in lichens (Darnley Gibbs, 1974). The lichenivorous browser might be defined as having a comparatively low trehalase activity, because a substantial part of its diet is of algal origin.

Herbo-fungivorous grazers: are able to digest all main food components of both green plants and fungi. This is the biggest guild found with 16 species of which five are genuine herbo-fungivores, because they have a relatively high enzyme activity of all three enzymes: *Nothrus silvestris*, *Nanhermannia elegantula*, *Phauloppia lucorum*, *Humerobates rostrilamellatus* and *Acrogalumna longipluma*. Lichenivory is also possible here, which probably holds for *P. lucorum* and *H. rostrilamellatus* (Seyd and Seaward, 1984). One species may be a transitional case to the fungivorous grazers: *Chamobates schützi*, and one species to the next guild: *Trichoribates trimaculatus*. The other species here show a relationship to the guild of the herbivorous grazers.

Table 4. 1. Fresh mass in μg (mainly data from the review of Luxton 1975, partly own data) number of specimens used in each analysis and in the blanks, activities of three carbohydrases (cellulase, chitinase, trehalase) expressed as μg end product $\cdot \text{mg}^{-1}$ mites $\cdot 4$ hours \pm 1 with standard error, based on four analyses and the main substrates the species were sampled from. Species are classified in feeding guilds. (1 potential lichenovorous grazer, 2 potential lichenovorous browser, 3 potentially feeding on blue-green algae)

Guild	fresh mass (μg)	number of specimens used per analysis	carbohydrase activities				specimens sampled from
			cellulase (μg glucose/ mg mite/ 4h)	chitinase (μg acetyl-glucosamine/ mg mite/ 4h)	trehalase (μg glucose/ mg mite/ 4h)		
Herbivorous grazers							
<i>Acropaccarus striculus</i> (C.L. Koch 1835)	18.0	14	34.8 \pm 32.3	0	0	Juniperus litter and moss	
<i>Pachiracarus ferrugineus</i> (C.L. Koch 1841)	20.3	14	16.0	0	0	Thuja litter	
<i>P. piger</i> (Scopoli 1763)	162.1	1	16.5 \pm 8.6	0	0	Quercus litter	
<i>Steganacarus magnus</i> (Nicolet 1855)	360.0	1	27.6 \pm 24.8	0	0	Quercus litter	
<i>Piatynothrus peltifer</i> (C.L. Koch 1839)	62.9	18	242.2 \pm 11.1	0	0	Fagus-Quercus litter	
<i>Trimalacanothrus novus</i> (Sellnick 1921)	30.9	12	219.5 \pm 25.2	0	0	Sphagnum (wet)	
<i>Xenillus tegeocranus</i> ((Hermann 1804)	158.9	2	97.6 \pm 15.5	0	0	moss on wet soil	
<i>Achipteria coleoptrata</i> (Linnaeus 1758)	40.0	6	89.4 \pm 20.2	0	0	Populus litter	
<i>Parachipteria punctata</i> (Nicolet 1855)	34.8	6	57.4 \pm 10.9	0	0	moss on soil	
Herbivorous browsers							
<i>Melanozetes mollicomus</i> (C.L. Koch 1839)	18.6	12	0	0	0	moss on soil	
Herbivorous grazers							
<i>Rhysotritia ardua</i> (C.L. Koch 1841)	57.0	5	51.0 \pm 21.1	5.0 \pm 0.2	10.7 \pm 1.3	Thuja litter	
<i>R. duplicata</i> Grandjean 1955	65.4	5	53.4 \pm 11.5	5.8 \pm 1.8	3.3 \pm 0.9	Thuja litter	
<i>Nothrus silvestris</i> Nicolet 1855	47.1	21	139.0 \pm 17.1	32.8 \pm 17.8	16.7 \pm 3.1	Fagus-Quercus litter	
<i>Camisia biurus</i> (C.L. Koch 1839)	134.1	2	92.9 \pm 20.3	13.7 \pm 3.8	8.2 \pm 0.4	Juniperus litter and moss	
<i>Nanhermannia elegantula</i> Berlese 1913	18.1	13	69.0 \pm 17.6	49.5 \pm 10.3	7.8 \pm 1.8	Quercus litter	
<i>Hermannia gibba</i> (C.L. Koch 1839)	94.2	3	193.4 \pm 78.6	24.7 \pm 10.6	9.9 \pm 0.9	moss on soil	
<i>Hermannella granulata</i> (Nicolet 1855)	75.3	3	136.4 \pm 29.4	7.0 \pm 3.8	6.8 \pm 1.1	Quercus litter	
<i>Phaetopia lucorum</i> (C.L. Koch 1841)	30.8	5	77.8 \pm 11.0	17.2 \pm 8.4	39.8 \pm 4.1	moss on tiles	
<i>Liebstadia similis</i> (Michael 1888)	19.4	12	393.4 \pm 36.6	7.6 \pm 2.5	32.8 \pm 9.0	grassland litter and soil	
<i>Chamobates schürzi</i> (Oudemans 1901)	8.3	30	24.6 \pm 2.7	21.6 \pm 11.2	70.9 \pm 12.2	Calluna vulgaris shrubs	
<i>Euzetes globulus</i> (Nicolet 1855)	31.0	1	106.9 \pm 36.3	30.7 \pm 10.7	26.0 \pm 4.6	moss on soil	
<i>Trichoribatetes trimaculatus</i> (C.L. Koch 1836)	34.4	5	176.9 \pm 124.1	9.6 \pm 3.0	68.2 \pm 17.7	grassland herbage	

continuation of Table 4.1

<i>Humerobates rostrilamelletatus</i> ¹ Grndj. 1960	60.9	5	102.0±38.6	30.4±14.9	36.8±3.6	Calluna vulgaris shrubs
<i>Achipteria nitens</i> (Nicolet 1855)	78.1	4	200.9±60.8	4.3±1.0	8.0±1.0	Thuja litter
<i>Acrogalumna longipluma</i> (Berlese 1904)	107.9	5	32.2±3.5	12.5±3.4	10.6±1.5	Thuja litter
<i>Pilogalumna tenuiclaves</i> (Berlese 1908)	82.4	5	20.0±12.3	5.2±2.1	3.9±1.8	moss on soil, Thuja litter
Opportunistic herbofungivores						
<i>Gamsia spiniferi</i> (C.L. Koch 1836)	115.0	2	144.0±20.8	0	27.6±11.3	Juniperus litter and moss
<i>Trihyopchthonielius excavatus</i> (Willm 1919)	20.0	12	108.3±8.4	0	4.6±0.3	Sphagnum (moist)
<i>Adoristes ovatus</i> ¹ (C.L. Koch 1839)	42.9	5	156.5±17.2	0	8.3±2.6	Juniperus litter and moss
<i>Carabodes labyrinthicus</i> ¹ (Michael 1879)	43.0	8	42.5±9.1	0	25.3±18.1	moss on bricks
<i>Tectocephus velatus</i> ¹ (Michael 1880)	4.2	60	171.3±18.8	0	18.1±10.1	Juniperus litter and moss
<i>Hydrozetes lacustris</i> ³ (Michael 1882)	32.3	8	176.5±8.5	0	13.9±3.4	Sphagnum (wet)
<i>Limozetes foveolatus</i> ³ Willmann 1939	3.8	60	189.4±18.4	0	6.6±1.1	Sphagnum (wet)
<i>Scutovertex minutus</i> ¹ (C.L. Koch 1836)	40.8	6	304.9±4.3	0	38.4±7.6	moss on bricks
Fungivorous grazers						
<i>Spatiodamaeus verticillipes</i> (Nic. 1855)	112.8	4	0	12.3±3.7	96.4±19.1	Quercus litter
<i>Everemaeus silvestris</i> (Forslund 1955)	18.8	10	0	10.6±4.5	7.3±2.2	moss on Quercus trunk
<i>Ramusella clavipectinata</i> (Michael 1885)	3.5	90	0	6.8±3.7	89.1±19.7	grassland litter and soil
<i>Oribatula tibialis</i> (Nicolet 1855)	14.8	12	0	15.5±5.1	76.4±24.4	Juniperus litter and moss
<i>Scheiorribates laevigatus</i> (C.L. Koch 1835)	28.1	8	0	10.5±3.2	55.2±13.8	grassland litter and soil
<i>Punctorribates punctum</i> (C.L. Koch 1839)	10.9	25	0	20.4±6.4	58.0±8.5	moss on soil
<i>Eupelops acromios</i> (Hermann 1804)	50.0	5	0	40.3±8.7	30.2±8.0	Calluna vulgaris, birches
<i>Galumna lanceata</i> Oudemans 1900	55.2	5	0	4.4±3.4	37.5±1.4	Vaccinium myrtillus shrubs
Fungivorous browsers						
<i>Paradamaeus clavipes</i> (Hermann 1804)	258.0	1	0	0	195.6±48.0	Juniperus litter and moss
<i>Ceratoppia bipilis</i> ² (Hermann 1804)	64.7	4	0	0	18.9±3.1	moss on tree trunks
<i>Licneremeus licnophorus</i> ² (Michael 1882)	1.2	80	0	0	8.0±0.9	Juniperus litter and moss
<i>Hemileius initialis</i> ² (Berlese 1908)	21.0	10	0	0	52.0±31.2	Juniperus litter and moss
<i>Chamobates borealis</i> ² (Trägårdh 1902)	6.6	30	0	0	52.8±6.3	Juniperus litter and moss
<i>Oribatella quadricornuta</i> ² (Michael 1880)	24.0	10	0	0	15.8±3.5	moss on soil, Thuja litter
<i>Tyrophagus similis</i> Volgin 1949 (Acaridida)	14.5	15	0	0	96.7±30.2	rye straw on soil
Omnivores						
<i>Hypochothonius rufulus</i> C.L. Koch 1836	22.1	11	187.4±129.1	111.5±27.4	0	Quercus litter

Opportunistic herbo-fungivores: are able to digest cellulose in litter and cell-walls of living green plants and trehalose in fungi. Their main food item probably consists of green plants. They can take advantage of periodic increases in fungal growth in their biotopes: a rather opportunistic feeding strategy. As has been pointed out already under the heading of the fungivorous browsers, ability to digest trehalose might also point to lichenovory. Especially the species from dry biotopes might be classified into the lichenovorous grazers. The guild of opportunistic herbo-fungivores can be divided in two groups based on the biotope they live in; a (semi)aquatic group (*Trhyppochthoniellus excavatus*, *Hydrozetes lacustris*, *Limnozetes foveolatus*) which might also feed additionally on Cyanophyta (containing both cellulose and trehalose), and a second group living in temporarily-favourable microbiotopes (moss on trees or stones, dropped cones of alder, etc.) (Wallwork, 1983) comprising *Camisia spinifer*, *Adoristes ovatus*, *Carabodes labyrinthicus*, *Tectocephus velatus*, and *Scutovertex minutus*, which may feed on lichens (also containing both cellulose and trehalose).

Omnivores: an unexpected guild to be distinguished on the basis of carbohydrases. However, the presence of cellulase activity clearly indicates herbivory and the presence of chitinase activity without trehalase activity is quite peculiar for fungal feeding only (able to digest the cell-wall, but not one of the major components of the cell-contents). Soil dwelling organisms having chitin and lacking trehalose as components are arthropods only. It is concluded, that species of this guild feed on plants and a chitin containing food source: arthropods. Hence, they are omnivores. One species was found: *Hypochthonius rufulus*.

DISCUSSION

The role of the gut microflora

One of the first questions arising in determination of carbohydrase activities is whether these enzymes are of animal or microfloral origin. Some authors have shown that some mites, such as *Achipteria coleoptrata* (Stefaniak and Seniczak, 1976) and *Oppia nitens* (Seniczak and Stefaniak, 1978), have a working microflora in the alimentary canal, able to digest more complicated polysaccharides. From an ecological point of view it is not very important whether it is the enzymes of gut bacteria that breakdown food components or the enzymes of the animal itself, provided that the microflora active in the alimentary canal is symbiotic in the

whole population of mites. The latter assumption can be held regarding the low standard errors in enzyme activity between samples of mites from different times and locations. Luxton (1972) used toluene as a bacteriostatic agent and measured little chitinase activity. As with carbohydrase activity by bacteria from outside the body toluene might also have stopped the chitinase activity of the gut microflora in such cases.

Induction of carbohydrase activities

Induction of a higher enzyme activity may be of importance. Stefaniak and Seniczak (1981) showed in *Oppia nitens* that the quality of food stimulated the microflora, which able to breakdown chitin. In the natural population chitin breakdown is low as is found in this study in the related *Ramusella clavipectinata*. However, when a species is not able to break down chitin, enzymes may not be induced despite the kind of food offered. In *Achiptera coleoptrata* for instance little chitin is broken down no matter which kind of food is offered (Stefaniak and Seniczak, 1976). The information, however, that some quantitative differences in enzyme activity might occur gives us a better idea of the menu of the field population, in which seldom only one food item plays a role. So carbohydrase activity gives a qualitative insight into the tools of a species, quantitatively it gives an idea of the recent use of such tools. The need to use all the tools (enzymes) is not always essential, and the rearing of species in the laboratory on easily-digestible food or on surplus food may yield positive rearing results, but does not give information on the field menu (Woodring, 1963). It will be no surprise when species reared in the laboratory on algae appear to digest fungi in the field. In the laboratory situation where food is plentiful there is no need for efficiency and probably many species will feed on the components easiest to digest (cell-contents). Walter (1987) and Walter et al. (1988) reported on carnivory among oribatids, which may be seen in this light. The enzymatic tools of the equipment of the species prove their value when food becomes scarce and efficiency is needed. An illustrative example may be the observation of Woodring (1963) of *Scheloribates laevigatus* feeding for several days on fresh-cut green grass, yet this species proved to be a fungivorous grazer in this study.

Comparison with current feeding guilds

The classification of oribatid mites in feeding guilds (Table 4.1) differs to some extent from the classification of Luxton (1972) and not only in nomenclature. There are differences among guilds, even when

Luxton's macrophytophages correspond with the herbivorous browsers and grazers together, his panphytophages correspond with both the herbo-fungivorous grazers and the opportunistic herbo-fungivores, and his microphytophages correspond with the fungal grazers and browsers here (which is certainly not the case because of Luxton's inclusion of algal feeders in the microphytophages). Both *Rhysotritia ardua* and *Hermaniella granulata* are macrophytophages according to Luxton (1972) in his review table, but appear to be able to digest chitin and trehalose and are thus herbo-fungivorous grazers. However, they resemble the herbivorous grazers. Kaneko (1988) found for *R. ardua* in his B plot that the guts contained 24% hyphae and therefore classified it as panphytophagous.

Some of the panphytophages reviewed by Luxton appear to be herbivorous grazers (thus without the capacity to digest fungal material): *Achipteria coleoptrata*, *Parachipteria punctata*, *Xenillus tegeocranus* and *Platynothrus peltifer*. Schatz (1979) found *Achipteria coleoptrata* to be macrophytophagous. Some others panphytophages reviewed by Luxton appear to be fungivores. *Hemileius initialis* is a fungivorous browser and Forsslund (1938) found mainly hyphae in its gut. The previously mentioned *Scheloriates laevigatus* is both in our study and in that of Woodring and Cook (1962) fungivorous, more precisely a fungivorous grazer. The same holds for *Galumna lanceata* (*G. cf. dorsalis* in Luxton (1972) and Van der Drift (1951), see Van der Hammen, 1952), which agrees with Van der Drift (1951).

A more peculiar species is *Tectocephus velatus* classified by Luxton (1972) as microphytophage, presented here as an opportunistic herbo-fungivore or maybe a lichenivorous grazer. This species has been a problem for many authors: Wallwork (1958) could not observe any feeding and found most guts empty, in his review some years later he classified it as macrophytophage (Wallwork, 1967). Behan and Hill (1978) classify it as microphytophage based on the gut contents of four specimens. Probably it depends on the environmental conditions what kind of food will be used by this species: a real opportunist. *Trhypochthonius tectorum* (Berlese 1896) classified by Luxton as a microphytophage is able to digest cellulose (cellulase activity: 132.2 ± 29.1 g glucose.mg⁻¹ mite.4 h⁻¹); activities of other enzymes could not be measured because too few specimens were available.

Another species for which many authors give different results is *Hypochthonius rufulus*. Riha (1951) and Tarman (1968) found it to be necrophagous, other authors microphytophagous (Hartenstein, 1962), Farahat (1966); and Wallwork (1967) reviewed it as a non-specialist. In our study it was found to be omnivorous because of its cellulase and chitinase activities. The species is equipped to feed on all kinds of plant and fungal material, but a high chitinase activity in the absence

of trehalase activity is illogical when the species should feed substantially on fungi. In this light it is interesting to compare the reaction of the symbiotic gutflora of *Oppia nitens* to a carrion diet: chitinase activity is far more developed as it is in the natural population (Seniczak and Stefaniak, 1978). The same process might occur in the natural population of *H. rufulus*. Support for this assumption is found in Behan-Pelletier and Hill (1983) where in the guts of adult specimens of this species up to 90% collembolan and mite fragments are recorded (means of 0-35%). Whether *H. rufulus* is a scavenger (*exuviae!*) or a predator is unknown.

Carbohydrase activities, especially those for the digestion of differentiating plant and fungal components, appear to give a solid basis for feeding guild definition. Quantitative data on enzyme activities permit transitions from one guild to another to be detected and help to find the most typical representative of a guild for further studies. It is expected that representatives of these feeding guilds will have distinctive interpretable effects on fungal activity in the decomposition of organic matter.

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Mites of different feeding guilds affect

decomposition of organic matter

SUMMARY. The impact of representatives of five feeding guilds of oribatid mites on microbial respiration during decomposition of *Avenella* litter was studied. Herbivorous grazers had no effect on microbial respiration; herbofungivorous grazers and fungivorous grazers had a stimulating effect on microbial respiration, while fungivorous browsers and opportunistic herbofungivores had an inhibiting effect on it. The guilds with stimulating effects on microbial respiration have in common the ability to digest chitin, a main component of fungal cell-walls. Chitin consists of nitrogen, the release of which may stimulate fungal growth and respiration. Addition of nitrogen in experiments stimulated microbial respiration, but the positive effect of a herbofungivorous grazer could not be demonstrated in experiments where extra nitrogen was added. It is concluded that stimulation of microbial respiration may be the result of the release of nitrogen from fungal cell-walls. Micro-arthropod grazing on fungi is discussed with respect to effects of micro-arthropod density, nutrient availability in the substrate and the nature of grazing. Next to these effects, temporal and spatial factors may have some influence on the eventual result of fungal activity on overall decomposition rates.

INTRODUCTION

In both community ecology and ecosystem ecology species are assembled in groups based on the supposed similar function exerted by the species within a group (e.g. Hawkins & MacMahon 1989, Walter et al. 1988). In animal ecology, Root (1967) proposed the guild concept for such groups. The concept of guild was used in soil biology since Schuster (1957) defined macrophytophages, microphytophages and panphytophages before the term guild was assigned to it. Also Berthet (1964), Lebrun (1971) and Luxton (1972) used this functional classification of oribatid mites and many authors did ever

since (e.g. Behan & Hill, 1978; Kaneko 1988; Wallwork 1983). At the time of that classification, the common opinion was that the function of soil fauna in decomposition was mainly fragmentation. Later Van der Drift and Jansen (1977), Hanlon (1981) and Hanlon and Anderson (1979) made clear that the grazing of fungi could also be a predominant function of micro-arthropods in decomposition of organic matter.

Many questions still are to be answered. How is decomposition of organic matter affected by the species abundance and distribution of fungi, by density and age of mycelium, by substrate physical and chemical properties, by extent and periodicity of soil moisture and finally what is the precise role of micro-arthropods. Fungus feeding Collembola can alter the competition between fungal species and consequently alter decomposition rates (Newell 1984b), when one of them is toxic or unpalatable for the collembolan (Parkinson et al 1977, 1979), or when the vertical distribution of one of the fungus species extends the range of the collembolan (Newell 1984a, 1984b). High densities of micro-arthropods tend to overgraze the fungi and decrease decomposition rates (Hanlon & Anderson 1979), but high substrate quality permits a strong growth of fungi which is not easily overgrazed by micro-arthropods (Hanlon 1981). Interesting also is how fungi are grazed, is all fungal material digested or are some parts left untouched which may eventually accumulate?

In Chapter 4 it is argued that the current classification of feeding guilds of non-predatory soil mites was not suitable to clarify their precise role in decomposition. To replace the current feeding guilds a classification was proposed based on digesting abilities of the species. Carbohydrase enzyme activities formed the basis of five major (species-rich) and two minor categories among oribatid mites. The five major categories are: herbivorous grazers, herbofungivorous grazers, fungivorous grazers, fungivorous browsers and opportunistic herbofungivores. The most important difference of these feeding guilds with the previously used micro-, macro-, and panphytophages is the distinction in digestion of fungal cell-contents only (browsers) or of both fungal cell-contents and cell-walls (grazers).

In this paper we demonstrate the influence of representatives of each of the five major feeding guilds on the process of decomposition of organic matter. Our hypothesis is that the herbivorous grazers will have no influence on decomposition rates and that the four guilds feeding in a specific way on fungi will affect decomposition rates guild-specific. Species digesting fungal cell-contents only may have a less stimulating or even inhibiting effect on microbial respiration (fungivorous browsers, opportunistic herbofungivores), while species digesting both fungal cell-walls and cell-contents are thought to stimulate microbial respiration (fungivorous and herbofungivorous grazers). The latter species may release nitrogen from the chitin in the fungal cell-walls, and can digest also inactive fungal

material, which may increase microbial growth rate. Both release of nitrogen in our experiments as NH_4NO_3 , as well as addition of a cell-wall digesting species may result in a stimulation of microbial respiration in aged mycelium. Effects will be interpreted from our knowledge of enzyme activities in the guts of the species used (Chapter 4).

MATERIALS AND METHODS

Mites were sampled from soil and moss cores using Tullgren-extraction with water in the collection jars. The jars were checked daily for the species to be used in the experiments. Five oribatid mite species were used in the experiments representing the five major feeding guilds (Chapter 4); the herbivorous grazer *Parachipteria punctata* (Nicolet 1855), the herbofungivorous grazer *Nothrus silvestris* (Nicolet 1855), the fungivorous grazer *Punctoribates punctum* (C.L. Koch 1840), the fungivorous browser *Chamobates borealis* Trägårdh 1902 and the opportunistic herbofungivore *Carabodes labyrinthicus* (Michael 1879).

The number of mites used per experiment depended on the size of the mite. In every experiment 0.5 mg adult mites were used. For *P. punctata* this corresponded with 15 individuals, for *N. silvestris* with 11, for *P. punctum* with 50, for *C. borealis* with 60 and for *C. labyrinthicus* with 12. The mites were placed in a small jar (5 cm diameter) on 6 g (dry mass) substrate. The jars were covered with a gauze of 40 μm mesh size.

The substrate was composed of 78% quartz sand (particle size 200-800 μm), 2% illite and 20% pulverized shoots of the grass *Avenella flexuosa* (L.) Dreyer (= *Deschampsia flexuosa* (L.) Trin.). The pulverized grass was composed of $32.4\% \pm 0.1$ lignin, $26.6\% \pm 0.1$ hemicellulose and $32.6\% \pm 0.5$ cellulose by mass, analyzed according to Goering and Van Soest (1970). Total amounts of N, P, and K were: $3.1\% \pm 0.1$, $0.2\% \pm 0.0$ and $2.4\% \pm 0.1$, respectively. Pulverization of organic matter was done to exclude possible fragmentation effects of mites on the organic matter. Fungal species were introduced with the organic matter, the species composition of fungi is therefore unknown, which may result in somewhat different levels of CO_2 production among series of experiments. Nematodes were not present in the jars. Bacteria and protozoans were present, their role is supposed to dominate the initial stage in the experiments (breakdown of simple sugars).

At the start of the experiment, the substrate in the small jar was moistened with de-ionized water, mites were added and the small jar was placed with another one containing 10 ml 0.1M KOH solution on wet filter paper to obtain high moisture conditions into a bigger jar (1 l) which was hermeti-

cally closed. CO₂ production was measured in the small jar with KOH, which was replaced two times per week. Titration with HCl revealed total amounts of CO₂ produced (Doelman & Haanstra 1979), blanks were used to tare the titration. The total amount of CO₂ per three or four days was calculated to CO₂ production.h⁻¹.g⁻¹ organic matter. Jars were kept at 15 °C.

Each series of experiments consisted of a jar with substrate and mites and a jar with substrate only (control) which were replicated five times. The blanks (jars without substrate and without mites) in every series of experiments were replicated three times.

In some later series of experiments nitrogen was added as NH₄NO₃ (Gams et al. 1987) to an amount of 2 g NH₄NO₃.l⁻¹. In these experiments 40 µl NH₄NO₃ was added at each replacement of KOH-jars, in total 8 times. Added nitrogen at the end was 224 µg N per jar. Total nitrogen per jar is about 37.2 mg, thus the added nitrogen is less than 1%.

Differences were tested for significance by analysis of variance (F-test). As measurements of respiration in a time-series are not independent, the last period of CO₂ production was used only to decide whether differences between control and treatment were statistically significant. Calculations made on earlier period should be considered as indicative for the start of divergence of control and treatment. We tested for differences in CO₂ production as late as possible in the experiments, because this stage may reflect the field situation more than an overall test on total respiration which includes the initial stage.

RESULTS

The herbivorous grazer, *Parachipteria punctata*, had no effect on the CO₂ production (Fig. 5.1a). It can be concluded that this mite, which is not able to feed on fungi, does not affect the rate of decomposition of *Avenella* leaves. CO₂ production of the mites themselves, as a result of feeding on the organic material is negligible compared to the microbial CO₂ production to be measured. Both species digesting fungal cell-walls, the herbofungivorous grazer, *Nothrus silvestris*, and the fungivorous grazer, *Punctoribates punctum*, had an eventual positive effect on the decomposition rate: in the presence of the mites CO₂ production was higher than in their absence (Fig. 5.1b, d). The two species however, not able to digest fungal cell-walls, the fungivorous browser, *Chamobates borealis*, and the opportunistic herbofungivore, *Carabodes labyrinthicus*, appeared to have an eventually negative effect on the decomposition rate: in the presence of the mites CO₂ production was lower than in their absence (Fig. 5.1c, e).

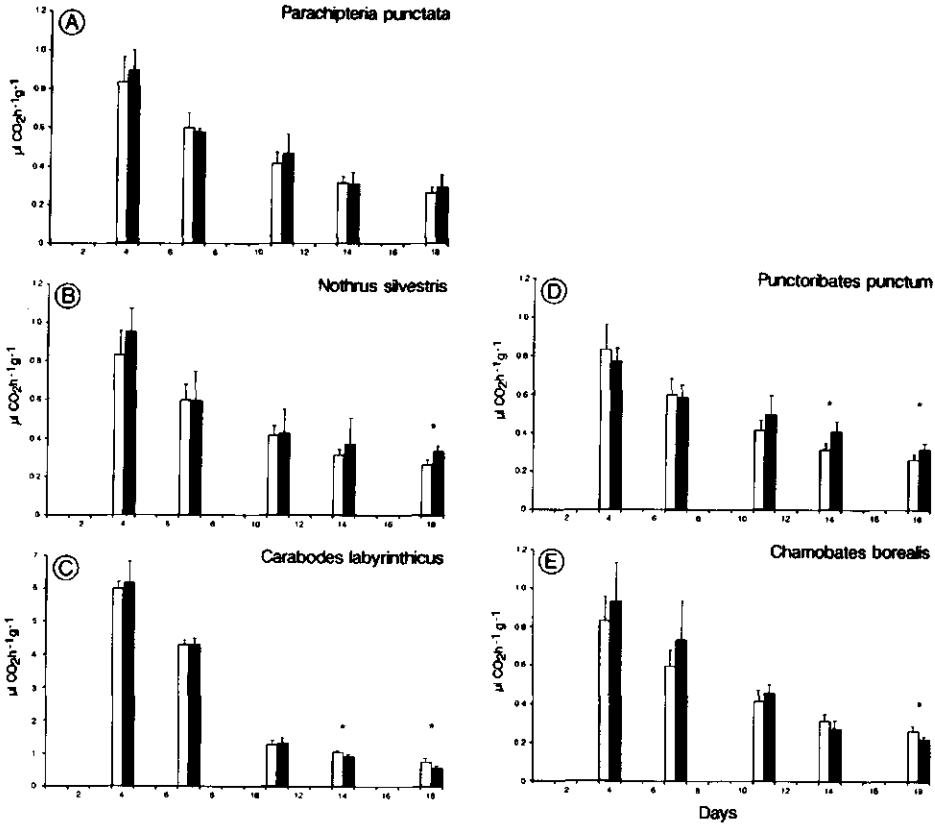


Figure 5.1. CO_2 production from pulverized *Avenella* leaves in the absence (white bars) and the presence (black bars) of (a) *Parachipteria punctata*, a herbivorous grazer, (b) *Nothrus silvestris*, a herbofungivorous grazer, (c) *Carabodes labyrinthicus*, an opportunistic herbifungivore, (d) *Punctoribates punctum*, a fungivorous grazer and (e) *Chamobates borealis*, a fungivorous browser. Asterisks above the bars of the last measurement reflect the statistical significance of difference: *, **; $p < 0.05$ resp. $p < 0.01$. Asterisks above earlier bars are to be considered as indicative for the start of divergence between treatment and control as they are not independent.

Microarthropod communities

It can be concluded that fungivory of mites affects CO₂ production. The one herbivorous mite had no effect on CO₂ production, unlike the four fungivorous mites. But the nature of the effect is completely different between grazers (herbofungivorous and fungivorous grazers) and browsers (fungivorous browsers and opportunistic herbofungivores) as explained in Table 5.1. Mites that can digest chitin had a positive effect on microbial respiration and as a consequence on decomposition rate; mites without that capacity had a negative effect.

Table 5.1. Cellulose, trehalase, and chitinase activities of representatives of five feeding guilds of mites and their effects on decomposition rate.

	cellulase activity	trehalase activity	chitinase activity	effect on decompos. rate	feeding guilds
<i>Parachipteria punctata</i>	+	-	-	o	herbivorous grazer
<i>Nothrus silvestris</i>	+	+	+	+	herbofungivorous grazer
<i>Punctoribates punctum</i>	-	+	+	+	fungivorous grazer
<i>Carabodes labyrinthicus</i>	+	+	-	-	opportunistic herbofungivorous
<i>Chamobates borealis</i>	-	+	-	-	fungivorous browser

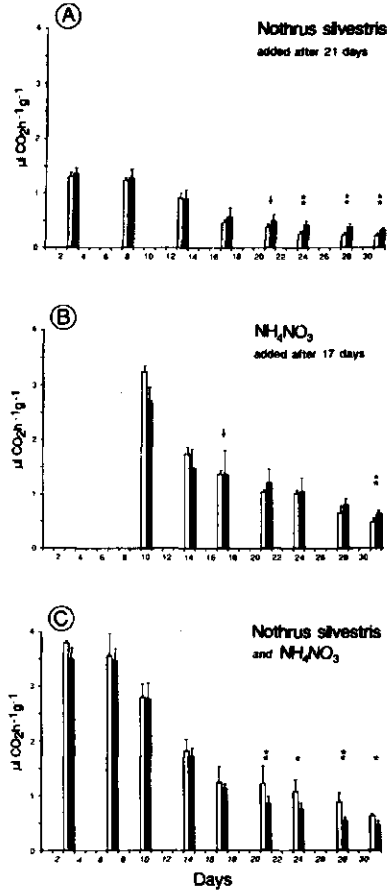


Figure 5.2. CO_2 production from pulverized *Avenella* leaves (a) in the absence (white bars) and the presence (black bars) of *Nothrus silvestris*, a herbofungivorous grazer, added after 21 days, (b) without (white bars) and with (black bars) NH_4NO_3 added after 17 days and (c) with added NH_4NO_3 in the absence (white bars) and the presence (black bars) of *Nothrus silvestris*. For the meaning of asterisks see legend of Figure 5.1.

So, mites digesting fungal cell-walls as well as cell-contents have a possibly positive feed back on microbial activity. Mites feeding on cell-contents only have a negative effect on fungal activity. The effect of fungivorous grazers or herbofungivorous grazers on a senescent fungal community is demonstrated in Figure 5.2a. In the presence of *Nothrus silvestris*, a herbofungivorous grazer, added after 21 days, the CO₂ production was significantly higher than in the series without mites. Cell-wall digestion by mites may have a positive feedback on fungal growth. Chitin is an important component of the fungal cell-wall, and can by definition be digested by fungivorous and herbofungivorous grazers.

Chitin contains of about 7% N by mass. If it is the nitrogen from chitin which stimulates microbial respiration, addition of available N must have a comparable positive effect. Figure 5.2b demonstrates the effect of addition of small amounts of NH₄NO₃ at intervals of three or four days from day 17 onwards. Eventually this addition had a positive effect on fungal activity, because CO₂ production was significantly higher at day 31. So both addition of a herbofungivorous mite, which digests chitin, and addition of NH₄NO₃ increased decomposition, probably by stimulation of microbial respiration.

If extra nitrogen is the clue in the stimulation of microbial respiration, then addition of NH₄NO₃ during the whole experiment should overshadow the positive feedback of the grazing of mites. The negative effect of fungivory should remain as has been shown in the browser case (*Chamobates borealis*, *Carabodes labyrinthicus* Fig. 5.1c, e). Figure 5.2c presents results from the final experiment with regularly added NH₄NO₃ in small amounts in jars with or without grazers. After three weeks, a period comparable to the first series of experiments, *Nothrus silvestris* had a negative influence on microbial respiration and thus on decomposition rate in the presence of added NH₄NO₃.

We conclude that it depends on the assimilation efficiency of the mites for nitrogen whether or not feeding on fungi stimulates CO₂ production rates. Furthermore, the positive feedback of two grazers (a fungivorous and a herbofungivorous one) can be explained from making nitrogen available through digestion of chitin, a main component of the fungal cell-wall.

DISCUSSION

Our choice to express mite density in mg mites is one out of several possibilities. The main point is whether this choice interferes with the final results or not. Both a large species (*Carabodes labyrinthicus*) and a small

one (*Chamobates borealis*) result in a negative influence on microbial respiration. Positive influence was found also in both a large species (*Nothrus silvestris*) and a small one (*Punctoribates punctum*). So, size of the mites, or numbers in the experiments provide no alternative explanation for the results obtained. Another expression for the impact of mites may be their metabolic activity. The sequence of metabolically most active (as measured by O_2 consumption at 10 °C) mites in descending order is: *C. borealis*, *P. punctum*, *P. punctata*, *N. silvestris*, *C. labyrinthicus* (data from Berthet (1964), Luxton (1975), Webb (1969) and Wood and Lawton (1973) on the listed or closely related species). Again this sequence provides no alternative explanation for the final results. Thus the density of mites, through the level of total metabolic activity, does not explain the outcome of the experiments.

The differences obtained between our series of experiments in the absolute level of microbial respiration may depend on small differences in substrate quality, or in microbial species composition. We have chosen to use the natural microbial species assemblage present on the organic matter to be sure that the organic matter forms the appropriate substrate for the microflora and the mite species may be familiar with the fungi in it as they originate all from litter in which *Avenella* leaves are present. The alternative: addition of few cultured fungal species has the advantage that microbial respiration is maybe more precisely reproduced among series of experiments, but has the risk that the introduced fungi are not the best decomposers of the selected organic matter or maybe unpalatable to one of the selected mite species.

Feeding of oribatid mites on fungi can lead to either a stimulation or an inhibition of decomposition depending on the nature of feeding. Digestion of fungal cell-walls next to cell-contents (grazing) leads to stimulation, digestion of cell-contents only (browsing) leads to inhibition at equal densities of mites expressed in mg mite per g organic matter. Hanlon and Anderson (1979) showed that density of the collembolan *Folsomia candida* influenced decomposition rate. High densities resulting in overgrazing inhibited O_2 consumption (which is equivalent to CO_2 production and thus decomposition in our experiments), while low densities had the opposite effect. Furthermore, Hanlon (1981) demonstrated that fungi grown at higher nutrient levels were stimulated by collembolan feeding, while fungi grown at lower levels were inhibited. So far, three factors influencing microbial respiration under feeding of micro-arthropods have been distinguished: the nature of feeding, the density of micro-arthropods and the nutrient level of the substrate. The effects of these factors are closely linked. Micro-arthropod grazing on fungi has a negative effect for fungi by damaging and decreasing fungal tissues next to a positive effect by releasing minerals, e.g. nitrogen, which may result in a faster fungal growth. The balance

Microarthropod communities

between the two effects determines the final result. Grazers may leave less damaged tissues as they digest almost all of the fungal tissues eaten, contrary to browsers which digest only fungal contents and thus will leave more damaged fungal tissue. Moreover grazers will also release more minerals from senescent fungal tissues compared to browsers and in this way stimulate fungal growth. Micro-arthropod density and nutrient availability for the microflora determine the balance between decrease and increase of microbial biomass. A high micro-arthropod density leads to an increased fungal destruction and thus to lower respiration. A high nutrient availability leads to a high fungal growth rate and consequently a more rapid recovery from grazing damage and thus a higher respiration. In Table 5.2 possible outcomes of interactions of the nature of micro-arthropod feeding, micro-arthropod density and nutrient availability are hypothesized. In this table stimulation of microbial respiration is more frequent with grazers than with browsers, at low micro-arthropod densities than at higher ones, and at higher nutrient availabilities than at lower ones.

Table 5.2. Hypothetical outcomes of the combined effects on microbial respiration of the nature of grazing (grazer or browser), density of fungal feeding microarthropods and nutrient availability for fungi.

nature of grazing	density of microarthropods	nutrient availability	possible effect on fungal respiration
grazer	high	high	±
		low	-
browser	low	high	++
		low	+
	high	high	-
		low	--
browser	low	high	+
		low	-

Patchiness in fungal distribution on the substrate leads to alternating high and low grazing pressure of micro-arthropods and may eventually result in an overall stimulating effect on microbial respiration (Bengtson & Rundgren 1983). Spatial and temporal effects which may be of minor importance in small scale microcosm experiments can be very important in nature. An illustration may be a microcosm experiment in which seedlings are grown. Assuming that the seedling takes advantage of the nitrogen released by micro-arthropod grazing, this nitrogen is not available for positive feedback on microbial respiration as argued before, hence a strong uptake of nitrogen by seedlings will inhibit the decomposition process, resulting in an unmeasurable effect in seedling growth. When there is no strong nitrogen uptake by seedlings, a measurable effect on seedling growth can also hardly be expected. Bååth et al. (1981) found no difference in growth of pine seedlings in the absence and presence of microbial feeding nematodes and mites. Kuikman and Van Veen (1989), however, demonstrated a 65% increase in mineralization and plant uptake of bacterial ^{15}N in a microcosm experiment with bacteria and protozoa as compared with bacteria only.

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6

Coexistence in soil microarthropods

SUMMARY. A spatial model is presented to evaluate the balances and compensatory effects between life-history traits, efficiency of use of resources, and tolerance for short-term, unpredictable environmental extremes in soil microarthropods. It appears that non-resource-related life-history traits, such as mobility, can compensate for less efficient use of food, resulting in the model in coexistence of more species than the number of available resources. The competitive exclusion principle appears to fail when mobility of the competing species is not unlimited. The question in ecology why are so many species present on a small scale should therefore be: why are so few species present where there appears to be room for more.

INTRODUCTION

Species diversity in soil microarthropods (mites and springtails) is usually very high. Moritz (1965) found on average 33 oribatid species per 500 cm² (range 23-45) in Central European forest soils. Sipel and Van de Bund (1988) found on average 45 oribatid species per 250 cm² (range 37-52) in unmanaged Dutch grasslands. For all soil microarthropods they found on average 108 species per 250 cm². Karppinen (1958) reported from Finnish forest soils an average of 19 oribatid species (range 8-26) on as little as 5 cm². All samples were taken up to a depth of 5 cm. This high species diversity on a very small scale seems to be at odds with the niche concept formulated by Hutchinson (1957) and Schoener (1989), which implies that species should minimize niche overlap in order to survive interspecific competition (Hardin 1960, Arthur 1984). So there should either be many resources in soil on a small scale, distinguishable for microarthropods (Anderson 1975), or microarthropods, belonging to different species, should be able to compen-

sate for inefficient use of, or not having access to, resources with (combinations of) other traits such as mobility, fecundity, spreading in oviposition, or tolerance to short-term unpredictable environmental extremes.

To evaluate the possible compensation of inefficient use of, or access to, resources by certain life-history traits, a simulation model was constructed which allowed soil mites to move freely over a grid and to use at most two types of food. It was hypothesized that an inefficient user of food can survive when it moves faster, or when it is more tolerant for periods of food shortage than an efficient user of food. Eventually, many species were hypothesized to be able to coexist on only two food sources.

Existing hypotheses on the coexistence of species such as the competitive exclusion principle (Hardin 1960) and Huston's (1979) general hypothesis on species diversity are discussed in light of the simulation results.

DESCRIPTION OF THE MODEL

A model with 132x120 grid cells was constructed. For each grid cell the following parameters were defined: probability of drought, probability of heat, probability of frost (meant as sudden occasions, not as predictable events in the season) and possibility of vertical migration to escape from these hazards (for small species only). The environmental factors were defined as a gradient on the grid, from a probability of maximal 10% per time step to 0% in steps of 1% per 8 rows or columns of grid cells (leaving about one third of the field unaffected). Next to the abiotic factors a biotic component, food, was defined for each grid cell. Food was offered in two independent forms. Amount of fungi was defined in units F , and in each grid cell F followed, independent of neighbouring grid cells, the growth function:

$$F_{t+1} = \frac{F_t * K_F}{F_t + (K_F - F_t) * e^{-r_F}}$$

where K_F is the carrying capacity of fungi and r_F the intrinsic growth rate of fungi. Initial values (F_t) for all grid cells were set at 6.0. The second food source was organic matter from green plants and algae in which two functions were defined. Algal growth was defined, and enlarged with annually falling leaves, as:

$$O_{t+1} = \frac{O_t * K_0}{O_t + (K_0 - O_t) * e^{-r_0}} + O_A * I(t_{\text{mod}52} = t_0)$$

where O is organic matter from green plants and K_0 and r_0 are their carrying capacity and intrinsic growth rate, respectively. A second input of organic matter on the soil surface was the annually ($I(t_{\text{mod}52} = t_0)$) falling leaves (dead organic matter): O_A , which coincided with mite reproduction. Time steps were weeks, to allow future comparisons with experimental data.

The initial number of mites was set at one hundred per species spread over the grid at regular distances. Individuals of second, third, etc. species were placed in neighbouring grid cells, initially. This resulted in a reproducible start of all simulations, initial equal availability of resources for all competing species, and competition all over the grid.

Mites feeding in the grid cells were grouped in guilds (Chapter 4). Six feeding guilds occurred in the model: herbivorous browsers (eating 0.2 units O per time step), herbivorous grazers (0.1 units O), fungivorous browsers (0.2 units F), fungivorous grazers (0.1 units F), herbofungivorous grazers (by preference 0.05 units F and 0.05 units O , but if either one of those is absent 0.1 units F or 0.1 unit O) and finally the opportunistic herbofungivores (by preference 0.2 units F , but in the absence of F the same amount of O). Grazers ate less than browsers because of their better enzymatic digestion capacity (they are able to digest cell walls next to cell-contents). The amount of food was eaten at each time step. However, when the amount of food was insufficient (less than the amount defined above) for the n^{th} mite in the grid cell, mites from n on may starve. The probability of death by starvation was:

$$VA = 1 - \exp(- \ln 2 / LD_{50})$$

per time step, where LD_{50} is the number of weeks after which half the population of mites died from starvation in experiments. The order of feeding for competing species was at random at every time step per grid cell.

Reproduction took place once every 52 time steps (one year), at t_0 , and was chosen to be thelytokous, that is every mite was a female and gave female offspring only. Egg-laying was either semelparous, all at once, or iteroparous following the functions:

$$R_t = Fc_t (1 - e^{-x^*t})$$

and

$$Fc_{t+1} = Fc_t - R_t$$

where R_t is reproduction at time t (weeks), F_t future reproduction potential at time t and x is the parameter of iteroparity, the smaller x the more iteroparous the reproduction will be.

The whole grid consisted of 132x120 cells. Mites were allowed to move from one grid cell to another. Individual mobility has been defined for random walk or phoresy. The random walk type let the mite move to the orthogonally neighbouring grid cells. The extent of this type of mobility was scaled from 10 to 100%, in steps of 10% probability of actual movement. The direction of the movement was random, because there is little evidence that soil mites head towards distant food sources.

The phoresy type of mobility let the mite move to any grid cell in the model. The probability to get to a certain grid cell depended on the amount of food present at the grid cell; a cell with a five times higher amount of food had an equally higher probability to be reached. The probability might be small, but never zero. This non-random direction of movement was derived from the directional migration to new food sources of the carriers of the phoretic mites, mostly flying insects. These insects are either able to locate a distant food source or the mites leave the carrier only on a favourable spot (Binns 1982). The phoresy modelled was adult carrier-unspecific phoresy as defined in Chapter 2.

Tolerance to environmental extremes was defined per species. The probability to die from frost, drought or heat depended on the probability of the hazard to occur at the grid cell where the mite was located. Species might survive environmental uncertainty either by tolerating or by avoidance. Small species were defined able to avoid frost, drought and heat because they can move into deeper soil layers (Metz 1971).

The probability to die, either from starvation or from environmental extremes, was calculated for every grid cell per species per time step. For every individual mite present in the grid cell, a random number was compared with the calculated probability to die, resulting in the death of the mites with random numbers lower than the calculated probability.

A listing of the simulation program is available from the author on request.

SENSITIVITY ANALYSES AND RESULTS

Food and feeding

Food availability determined the population sizes in the model. Increase of food as determined depended on two parameters: r_f or r_0 , the rate of increase, and K_f or K_0 , the carrying capacity, of fungi respectively algae.

The impact of these parameters on numbers of either fungivorous or herbivorous mites is shown in Figure 6.1 for various values of r_F or r_O and in Figure 6.2 for various values of K_F or K_O . From these figures it can be concluded that the rate of increase of food, rather than the carrying capacity, determined population size eventually. Thus food in this model is always limited (and limiting)! Default values of r_F , r_O , K_F , and K_O for the simulations to follow are given in Table 6.1. The default mite species is artificial and is constructed on the most simple and average traits of mites. Each time step in a figure refers to an average of 10 simulation runs.

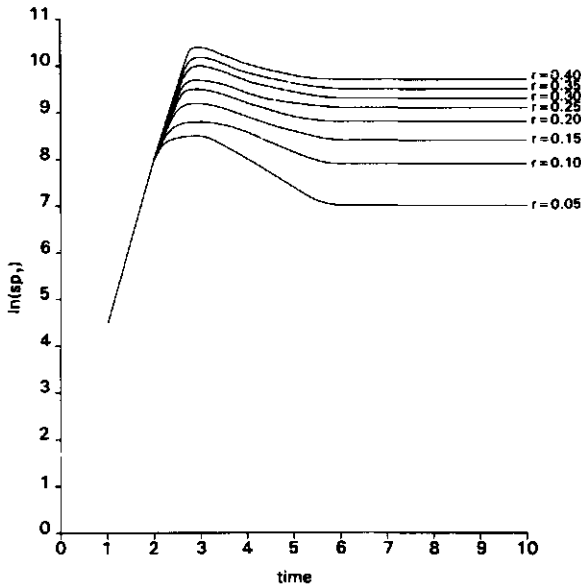


Figure 6.1. Population size during the first ten generations of a fungivorous grazer at different values of the fungal growth rate (rf), or a herbivorous grazer at different values of increase of algae and organic matter (rom), both referred to in the figure as r .

In the former section different feeding guilds were defined on the basis of differences in the amount of food used. Browsers were defined as less efficient feeders than grazers and some guilds exploited both fungi and algae. So it is to be expected that the feeding guild also determines the population size in single species runs. Figure 6.3 presents population sizes of species belonging to different feeding guilds. Browsers reached the

Microarthropod communities

least high numbers, grazers reached higher numbers and ability to use two food types increased numbers even more for both the browser type (opportunistic herbofungivore) and the grazer type (herbofungivorous grazer).

Table 6.1. Default values used in the simulation experiments.

Initial number of mites	100
Individual mobility	10
Feeding guild	fungivorous grazer
Growth rate r_f , r_{om}	0.25
Carrying capacity K_F , K_O	9
Annual input of organic matter (O)	6
VA (chance to die in absence of food)	0.100
Reproduction (number of eggs)	36
Iteroparity parameter	5.00 (semelparity)
Tolerance to drought	tolerant
" " frost	tolerant
" " heat	tolerant

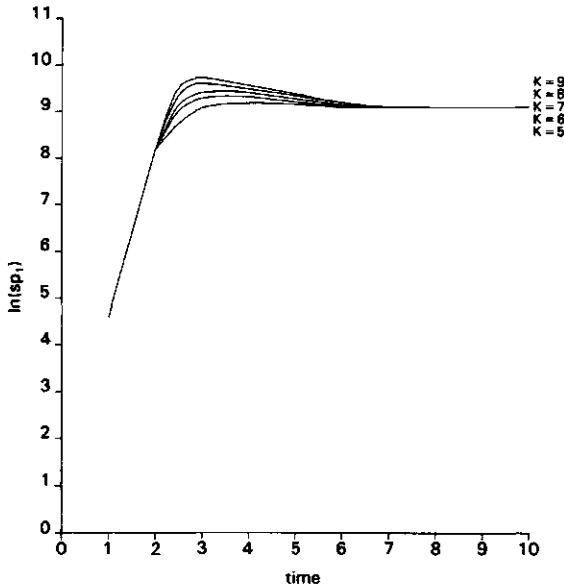


Figure 6.2. Population size during the first ten generations of a fungivorous grazer at different values of the fungal carrying capacity (K_F), or a herbivorous grazer at different values of the algal carrying capacity (K_O), both referred to in the figure as K .

The period a species could live without food, i.e. the probability to die (VA) in the absence of the required amount of food, had some influence on population size (Fig. 6.4). Compared, however, to the influence of feeding guild or rate of increase of food, VA had a small effect on numbers.

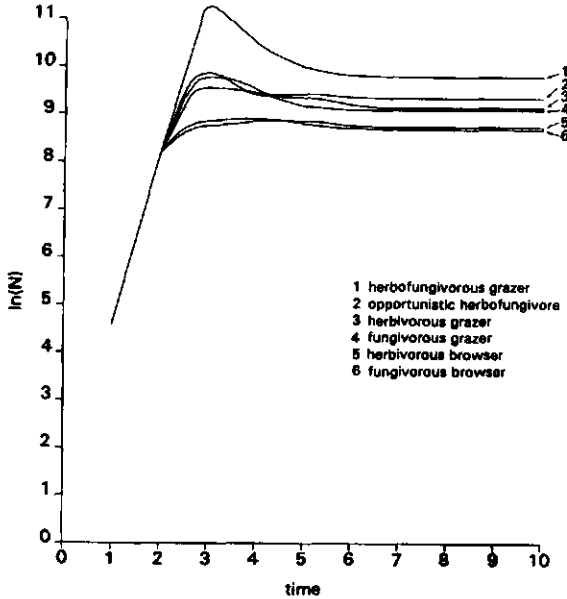


Figure 6.3. Population size during the first ten generations of species belonging to different feeding guilds; fungivorous grazer, or browser, herbivorous grazer, or browser, herbofungivorous grazer, and opportunistic herbofungivore.

Individual mobility

The parameter of individual mobility of the random walk type ranged from 1 to 10, in steps of 10% probability of actual movement. Figure 6.5 presents equilibrium population size versus degree of mobility. Differences in numbers due to differences in mobility were of a comparatively small magnitude. However, combination of low mobility and high VA parameter resulted in small populations (offspring would result in local high densities, a depletion of food and consequently because of the high starvation rate a minimum of survivors among that offspring).

Fecundity

Figure 6.6 (line 3) demonstrates equilibrium population sizes at increasing fecundities. Not shown in this figure is that the equilibrium was reached at a later stage at lower fecundities. The shape of this function is rather peculiar: as a matter of fact it is composed of two functions (Fig. 6.7). Survival rates of immatures depended on local density and survival rates decreased with increasing density, because mobility was limited to orthogonal cells (Fig. 6.7: line A). A higher local number of immatures increased the probability that some moved relatively far from the egg deposition place and increased their probability to survive (Fig. 6.7: line B). Together both functions show a dip at moderate fecundities. When mobility was set to phoresy, the dip disappeared, due to the disappearance of the higher population numbers at low fecundities in case of restricted mobility (Fig. 6.6: line 2). Halving the default mobility resulted in a downwards rotation of line B in Figure 6.7 which resulted in the function presented in Figure 6.6 (line 4).

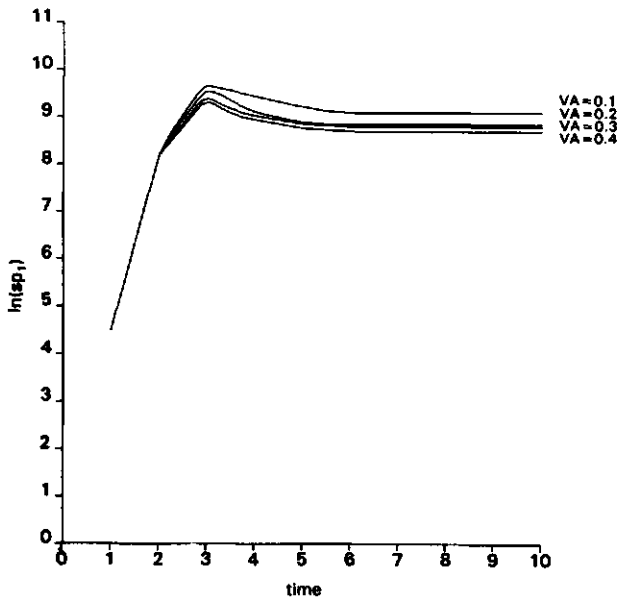


Figure 6.4. Population size during the first ten generations of a fungivorous grazer at different values of tolerance to food shortage (VA).

Iteroparity (spreading oviposition in time; $x=0.05$) resulted in increased population numbers because local interspecific competition decreased.

The dip at moderate fecundities, however, still existed (Fig. 6.6: line 1). This dip vanished when spreading of oviposition was defined both in time and in place (when individuals were able to oviposit in different cells at different times). So fecundity influenced equilibrium population size. The extent to which, was influenced by iteroparity or semelparity and by the individual mobility of the species.

Abiotic factors

Species in the model, intolerant to dry, cold or hot conditions were not present in areas of the defined field where the frequency of these harsh conditions in the grid cells was high. In areas having moderate frequencies of any of these harsh conditions intolerant species had a moderate population density. As a result the area available was decreased for these species.

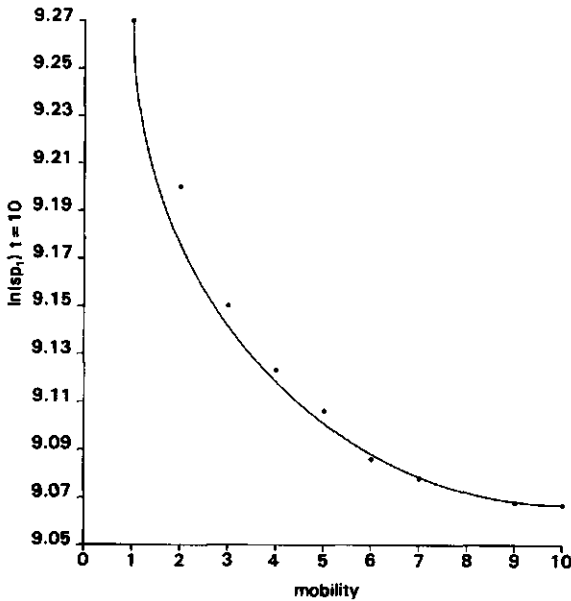


Figure 6.5. Equilibrium ($t=10$) population size of a fungivorous grazer at different values of individual mobility of the random walk type.

Interaction of two species

The competitive ranking of the six feeding guilds entails few surprises.

The fungivorous grazer was a better competitor than the fungivorous browser, because of the lower amounts of food the former ingested. The same held, *mutatis mutandis*, for herbivorous grazers and browsers. In general species able to use two food types were better competitors than those confined to only one. The herbofungivorous grazer was the best competitor. However, the opportunistic herbofungivore drove either fungivorous or herbivorous browsers to extinction, but had a stable coexistence with either fungivorous or herbivorous grazers (stability depended on the ratio of units F and O which is default). The high demand for food of the opportunistic herbofungivore was compensated for by its ability to change food types and it could coexist with a fungivorous grazer by feeding on algae. It was able to coexist with a herbivorous grazer, because it preferred feeding on fungi. So an inefficient user of food may compensate with other factors to coexist with the more efficient user of food.

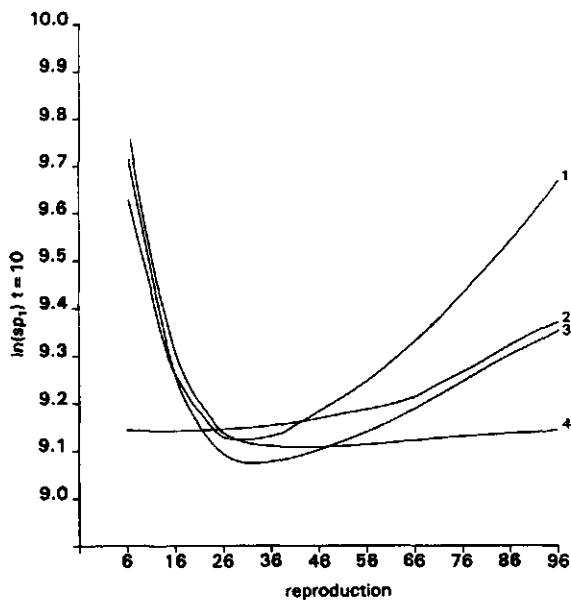


Figure 6.6. Equilibrium ($t=10$) population size of a fungivorous grazer at different fecundities (3), the same when mobility is restricted (4), the same when mobility is unlimited (2), and when mobility is restricted and oviposition is iteroparous (1).

In the next series of simulations a fungivorous grazer (the efficient user of food) competed with a fungivorous browser. The extra amount of food the browser ingested (defined as twice the amount ingested by the grazer)

the browser ingested (defined as twice the amount ingested by the grazer) could be used in several ways: a higher fecundity, a higher mobility, or a longer starvation period. In the first series of runs the inefficient user of food (the browser) might compensate with a higher fecundity. Figure 6.8 demonstrates the outcome of the competition in terms of log ratio of numbers ($\log (sp_1+1)/(sp_2+1)$). Even when the fecundity of the browser was only a little higher than the grazer, it had an initial advantage but eventually the grazers won. Only when reproduction of the browser was at least twice that of the grazer it might coexist for a longer time (but not infinitely). Figure 6.9 presents the log ratio of grazers and browsers with increasing mobility (random walk type) of the browser. An initial advantage of the browser was present when it moved at least seven times faster. Permanent coexistence was possible when the browser moved nine times faster than the grazer. In the third series of runs the browser might survive longer in the absence of the required amount of food. Figure 6.10 presents the log ratio of the population sizes in these runs. Already when the browser could survive 1.5 times longer than the grazer in the absence of the required amount of food it would show both an initial advantage and permanent

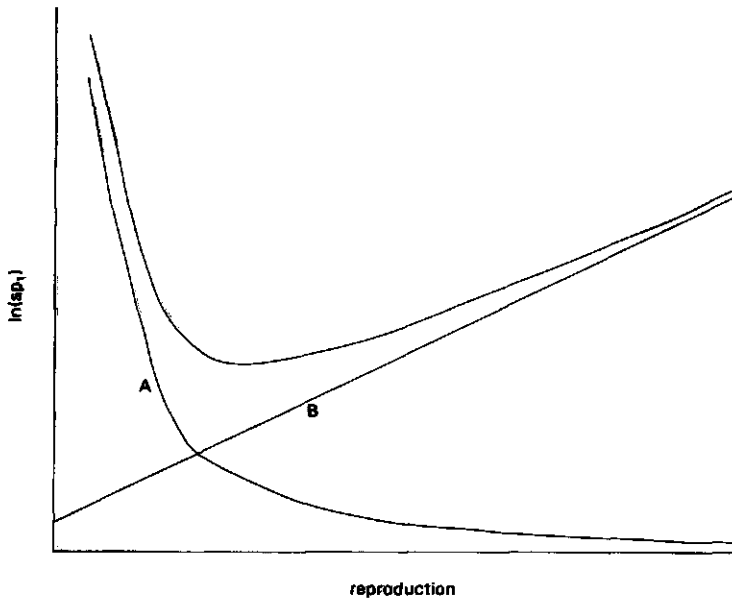


Figure 6.7. The combined effect of the local survival probability (a) with the probability of some individuals to move away (b), resulting in the function presented in Figure 6.6 (lines 1 and 3).

Microarthropod communities

coexistence. When it was able to survive more than twice as long as the grazer, it would outcompete the grazer. The parameter VA appeared very important in competition, a result which could not be concluded from the sensitivity analysis in single species runs.

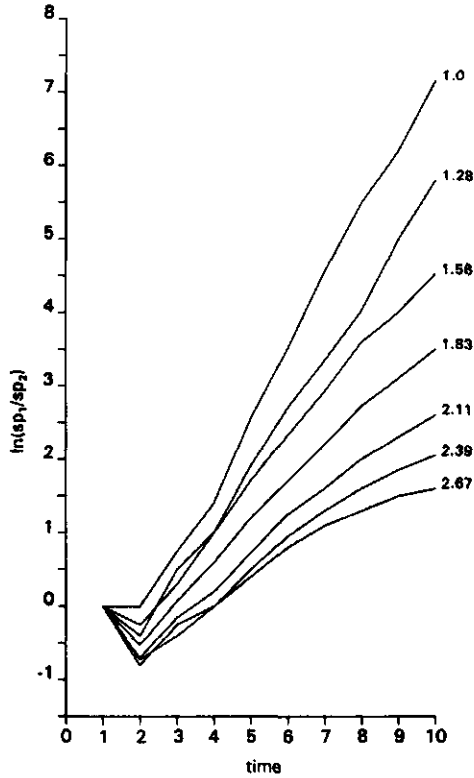


Figure 6.8. The log ratio of numbers of a fungivorous grazer (sp1) and a fungivorous browser (sp2) during the first ten generations; fecundity of the browser varies from 1.00 to 2.67 times the one of the grazer.

SIMULATION OF ECOLOGICAL PRINCIPLES

Huston's hypothesis on species diversity

Huston (1979) pointed out that under conditions of frequent disturbances potentially competing species do not manage to reach such a population

level that species may outcompete one another, because food or other resources are not limiting. In the model a fungivorous grazer and a fungivorous browser competed for food along a gradient of increasing probabilities of drought. Both the grazer and the browser were intolerant to drought and suffered from an increasing mortality probability along the gradient. Moreover, when the fungivorous grazer reached its maximum population density, the browser was outcompeted as has been shown before. Figure 6.11b shows the numbers at equilibrium of both species along the gradient. The fungivorous browser could survive only in the part of the gradient where numbers of grazers were lowered because of the increased probabilities of mortality and at the same time the probabilities of

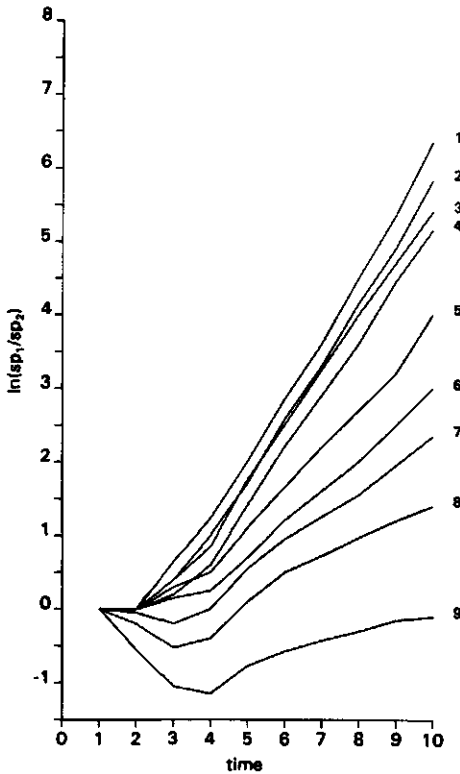


Figure 6.9. The log ratio of numbers of a fungivorous grazer (sp_1) and a fungivorous browser (sp_2) during the first ten generations; individual mobility ratio of browser/grazer varies from 1 to 9.

Microarthropod communities

mortality of both species were still low enough to survive. So, these simulations support Huston's hypothesis on species diversity. When the browser is given twice as high a mobility as the grazer, it is able to extend its range considerably (Fig. 6.11c).

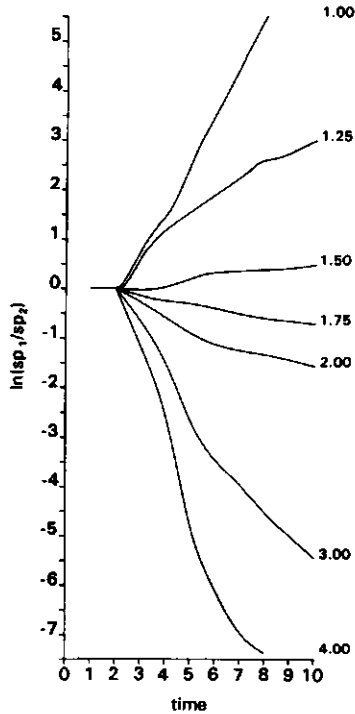


Figure 6.10. The log ratio of numbers of a fungivorous grazer and a fungivorous browser during the first ten generations; tolerance to food shortage of the browser varies from 1 to 4 times that of the grazer.

Identical niches

The model gives the opportunity to compare species defined to have identical niches, as stated in the competitive exclusion principle (Hardin 1960), even when this phenomenon may not exist in nature (Arthur 1987). The competitive exclusion principle is not falsifiable in nature because any difference may cause species coexistence. The principle is based on Lotka-Volterra equations in which mobility is not expressed. It implies that every individual of a population competes with every individual of the other population, which means that mobility is unlimited. To test the competitive

exclusion principle under the conditions it is derived for, two species were defined identically (both fungivorous grazers) and having unlimited mobility (they could reach any locality in the area in each time step). Just as predicted by the principle one of them went extinct. The probability was found to be once per 141 generations. In some computer simulation runs one already got extinct after some tens of generations.

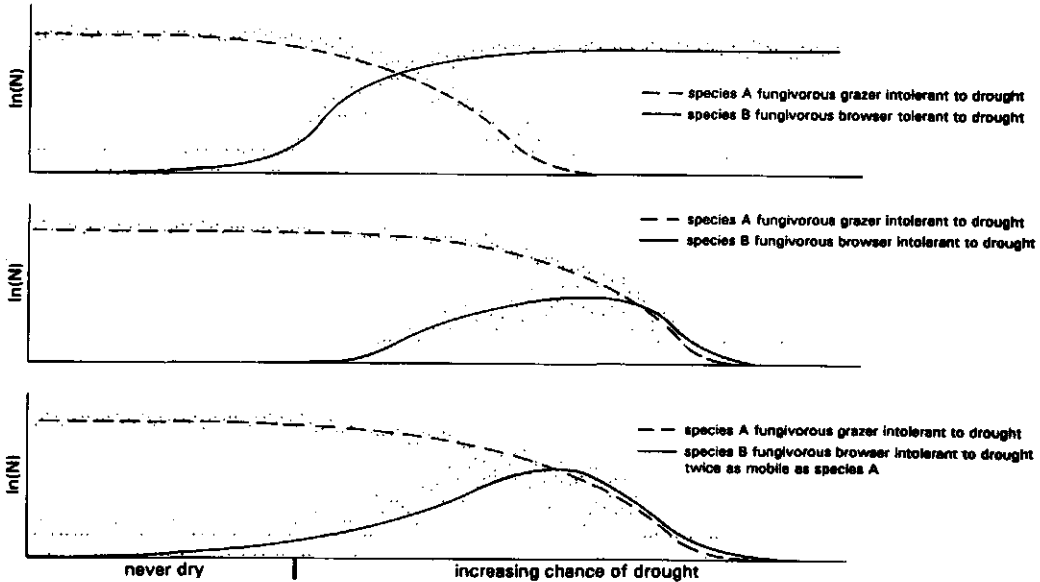


Figure 6.11. a) Log numbers of a fungivorous grazer, intolerant to drought, and a fungivorous browser, tolerant to drought, along a gradient with, from left to right, increasing probabilities of drought. b) Log numbers of a fungivorous grazer and a fungivorous browser, both intolerant to drought, along the same gradient as a. c) Log numbers of a fungivorous grazer and a fungivorous browser, both intolerant to drought, along the same gradient as a. The browser has twice as high a mobility as the grazer.

Mobility of species, however, is not unlimited in reality. The question is whether the principle also holds when mobility is restricted. Carrying out the same simulation with the same identically defined species but now having a restricted mobility (random walk type value 10) decreased the probability of extinction of either one of them to once per 66 million generations. In practice this implies infinite coexistence in case of restricted mobility. Thus the competitive exclusion principle does not apply.

Microarthropod communities

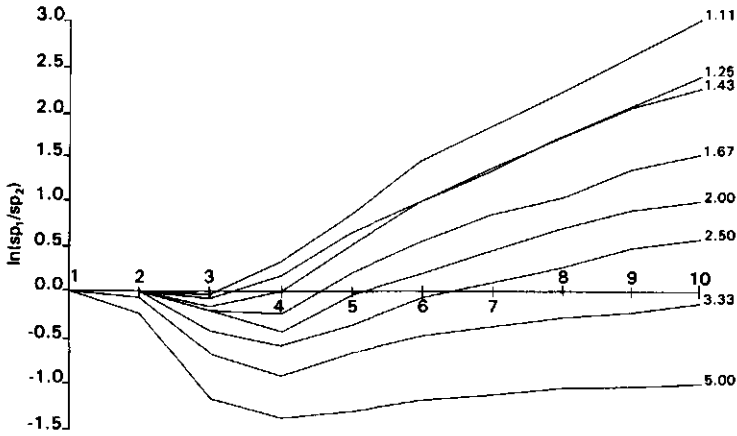


Figure 6.12. The log ratio of numbers of a fungivorous grazer (*sp1*) and an opportunistic herbo-fungivore (*sp2*) in the presence of a herbivorous grazer during the first ten generations; individual mobility of the opportunistic herbofungivore varies from 1.1 to 5 times that of each of the grazers.

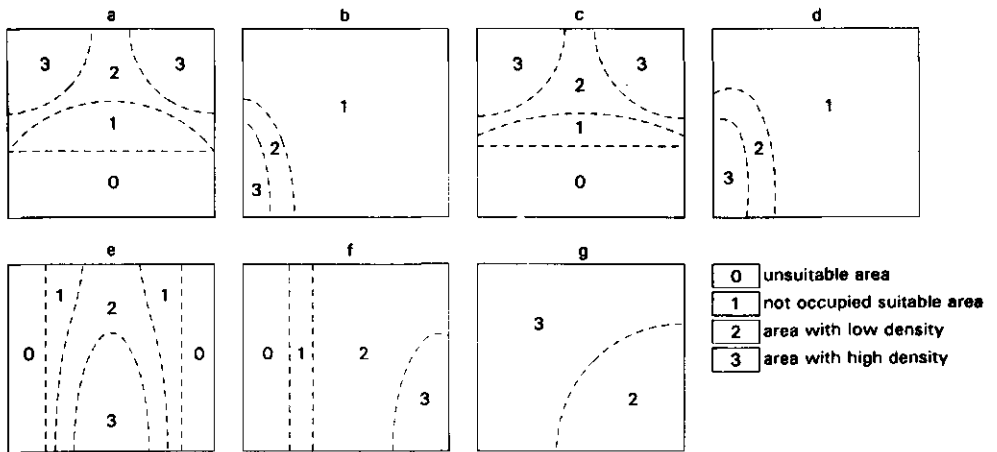


Figure 6.13. Distribution over the grid of seven coexisting species using only two food sources. Per species four areas are distinguished: unsuitable areas (0), suitable but not occupied areas (1), areas with low population densities (2), and areas with high population densities (3). Species definitions (a-g) are given in Table 6.2.

Three species systems

Increasing the number of competing species in the model leads to an enormous increase of potential combinations of species co-occurrences. Only some of the most interesting combinations are summarized here.

Given a fungivorous grazer and a herbivorous grazer, what qualities must a third species, feeding on both food types, have to be able to survive, or even to outcompete the two others. Adding a herbofungivorous grazer to the two grazers resulted in a slow but steady increase of the herbofungivorous grazer at the cost of the two food specialists. When instead of a herbofungivorous grazer an opportunistic herbofungivore (browser-type) was introduced, which consumes more food than the grazers, the browser was found to be gradually outcompeted by the grazers. However, when the browser had a greater mobility then it had good probabilities to coexist with both grazers. Figure 6.12 shows the log ratio of the fungivorous grazer to the opportunistic herbofungivore in the presence of a herbivorous grazer. Due to the definition of the opportunistic herbofungivore it affected mostly the fungivorous grazer. Comparison of Figure 6.12 with Figure 6.9, where a fungivorous browser with increasing mobility competed with a fungivorous grazer, shows that already a little higher mobility of the opportunistic herbofungivores over the two species of grazers permitted coexistence. So ability to use more types of food can overcome a bigger need for food per feeding site, when it is combined with an increased mobility. Here again, coexistence of more species than available resources is possible.

Table 6.2. Traits of seven species competing together for two types of food. Default values are given in Table 6.1, reproduction is in eggs.female⁻¹.year⁻¹.

Feeding guild	reproduction	mobility	drought	frost	heath
a fungivorous grazer	default	5	-	+	+
b fungivorous browser	default	5	+	+	+
c herbivorous grazer	default	5	-	+	+
d herbivorous browser	default	5	+	+	+
e herbofungivorous grazer	16	3	+	-	-
f opportunistic herbofungivore	default	default	+	-	+
g fungivorous browser	16	phoretic	+	+	+

Multispecies systems

From the above results coexistence seemed possible for more species than the number of available resources. Moreover, when mobility was restricted, species with identical niches could coexist, making the number of species in a community theoretically almost equal to the maximum number of individuals.

Six feeding guilds have been distinguished and defined so far. In the former section differences in the use of food or the needed amount of food could be compensated for by other traits. Now in one simulation experiment representatives of all six guilds have been made to compete for two types of food: green plants (algae or organic matter) and fungi. Table 6.2 presents the characteristics of these species. Figure 6.13 presents the distribution of the species in the simulated area. Distinction has been made between unsuitable areas (e.g. the frequency of drought is too high for the drought intolerant species) potentially suitable areas which are not occupied (due to strong competition), areas with low densities and finally areas with high densities. It appeared still to be no problem for one more species next to the six original feeding guild representatives to survive in the model. This species was obligately phoretic and had a rather low overall density; with respect to its feeding behaviour it belonged to the fungivorous browsers. Note that on all spots in the simulated field three or more species coexist. Bearing in mind that other representatives of the feeding guilds with roughly similar traits might also survive because of the restricted mobility of almost all species, we may conclude that this simple model theoretically allows coexistence for more species than available resources.

DISCUSSION

A model as presented here allows simulation of real soil microarthropod species compositions. The parameters needed for this model can be obtained relatively easily, assuming independence among parameters (e.g. between reproduction and drought conditions). By varying one variable at a time the sensitivity of the model for the parameters was estimated. It appeared that especially the period a species can survive without food (Fig. 6.10) is to be measured as precisely as possible. However, many more data are needed to simulate real species communities and even with precisely measured data the model will not give a realistic prediction about community composition because of the following limitations of the model. The difference between browser and grazer is defined in this model as a difference in need for

amount of food, an assumption which can only be true when both species are about equally sized with an about equal metabolic rate, which is a simplification of reality. Another factor not specified in this model is the availability of food. The fact that small species can obtain their food from small cavities where other species cannot reach it (except Pelopidae with specially shaped chelicerae) is not considered. So the step to the field still will be rather big. A comparison with field data (Siepel 1992), therefore, is quite precarious due to other differences among species than use of food only. Moreover, these differences in reproduction, generation times, and mobility may often be linked to the use of food. Species comprised in the categories 'fungivorous browsers' and 'fungivorous grazers' may be comparable with respect to their life-history in the mentioned study. In (semi-)natural grasslands the proportion of fungivorous grazers is much higher than that of fungivorous browsers, as was shown in the model. All species comprised in 'herbofungivorous grazers' have much longer generation times, lower fecundities, and lower mobilities than the average fungivorous browser or grazer, or opportunistic herbofungivores.

The choice for thelytoky as the type of reproduction was made both to keep the model simple and clear and the relative importance this type of reproduction has in soil mites. Simulating sexual reproduction in a model based on individuals would give some extra difficulties, such as for example the longevity of spermatophores deposited by males. These spermatophores are deposited with and without presence of females, and are subject to predation and destruction by moulds (Trávníček, 1979). Although it is a simplification of reality the choice for thelytoky instead of sexual reproduction is probably not essential for the results of the simulations.

On the other hand, the model served well the purpose of testing theories. It was shown that the model supported the species diversity hypothesis of Huston (1979), but the competitive exclusion (Hardin 1960) only when mobility was unlimited, as implicit in the equations of Lotka and Volterra. Restricting mobility showed that competitive exclusion failed. The parameter value (1-10) of mobility did not influence the outcome of the simulation very much. The fact that individuals were restricted to go step by step through adjacent fields was the most important. Step by step movements are the most common in nature in most microarthropods and also in other groups of organisms, although the real size of the grid cells with their own independent conditions may be bigger. Thus, the competitive exclusion principle may at best be approached by the most mobile species.

In predator-prey interactions the recognition of the importance of spatial variability is quite common. Nachman (1987a, b) found a stabilizing global effect in acarine predator-prey systems with a characteristic 'hide-and-see' pattern, but with local instabilities. Kareiva (1987) stressed the importance of an organisms dispersal behaviour (behavioural response

to fragmentation) for clarifying the unexpected destabilization of predator-prey interactions in ladybirds and aphids on golden rods. This behavioural response again is in fact the mobility between patches. Hassell *et al.* (1991) show in model simulations overall persistence of hosts and parasitoids in a subdivided environment in host-parasitoid associations. Hosts then are aggregated and constant fractions of both hosts and parasitoids may move to neighbouring patches, even with randomly searching parasitoids and without explicit density-dependency. Atkinson and Shorrocks (1981) pointed earlier to the importance of divided and ephemeral resources for the high species diversity in *Drosophila* species, which as a matter of fact means a restriction in mobility for the larvae. Larvae are not able to move from one ephemeral resource to another. In a cage experiment Shorrocks (1991) actually demonstrated that the inferior competitor may persist with the superior species when the space is divided in ephemeral patches, whereas the inferior competitor is eliminated in the same but undivided space. Both in predator-prey interactions, host-parasitoid associations and competition between species, mobility appears to be of great importance for the persistence of the species in different ways.

Next to the importance of mobility the model has shown that the original niche concept (Hutchinson 1957, Schoener 1989) is too restricted. It appeared that species may compensate the less successful use of the same resources than better competitors with non-resource related traits such as the fecundity, the maximum starvation period, and individual mobility. So, the question put forward by some authors (e.g. Silvertown 1987) how so many species can coexist while they are competing for a far lower number of resources is solved on the basis of this work and others (Janzen 1970, Huston 1979, Tilman 1982). In general, coexistence may occur when species cannot reach a level of total exploitation of resources either through abiotic factors (e.g. disturbances: Huston 1979) or through biotic factors such as predators (Janzen 1970), resource ratios (Tilman 1982), and life-history compensations of differences in exploitation levels (this study). Moreover, coexistence may occur when species have a restricted mobility (this study). After all, we may wonder why there are so few species rather than why there are so many.

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Competitive exclusion is not a general ecological principle

The principle of competitive exclusion (Hardin, 1960) is thought to be the most general one in ecology (Arthur, 1987). Of two species occupying the same niche, one will outcompete the other when resources are limited. The principle seems at variance with the overwhelming species diversity, particularly in plants and invertebrates. Ecologists working on these taxa, therefore proposed several additional hypotheses that allow by-passing the principle. This was done either by weakening the impact of competition, or by distinguishing extra niche dimensions to reduce niche overlap. The crux of the principle, however, is basically formed by the equations of Lotka and Volterra which implicitly assume unlimited individual mobility.

That assumption may explain the difference of opinion between ecologists adopting the principle (MacArthur & Levins 1967, Pianka 1973, Cody 1974, Gurnell 1985), often working with mobile vertebrates, such as reptiles, birds, and mammals, and those reluctant to adopt the principle, often working with less mobile invertebrates or plants. The latter group, also often struggling with the niche concept and derived principles, formulated new concepts on high species diversity on a small scale with few, limited resources (Silvertown 1987, Huston 1979, Connell 1971, Janzen 1970, Tilman 1982, Grubb 1977, Shmida & Ellner 1984, Taylor & Taylor 1977, Shorrocks *et al.* 1984, Warner & Chesson 1985).

Their question is, how can many species coexist without outcompeting each other? Several hypotheses by-passing the competitive exclusion principle have been formulated to explain the observed species diversity. Species with the same niche may coexist when none of them reaches its limit in population numbers due to disturbances (Huston 1979). In host/prey aggregates, predators or diseases may prevent a host/prey from reaching such high densities and hence from outcompeting other species (Connell 1971, Janzen 1970). According to the resource-ratio hypothesis (Tilman 1982) two species can coexist and use the same resources without outcompeting each

other, because of differing resource exploitation efficiency. Juveniles may require different resources than adults resulting in niche separation in the more vulnerable juvenile phase (Grubb 1977). According to the aggregation hypothesis (Shmida & Ellner 1984) intra-specific competition within aggregates is more important than inter-specific competition, thus decreasing the role of the latter (but see Connell 1971 and Janzen 1970). In insects, competition may be reduced by spatial factors (Taylor & Taylor 1977), especially in ephemeral and discrete resources (Shorrocks *et al.* 1984). The storage-effect hypothesis (Warner & Chesson 1985) focuses on temporal aspects: competing species can coexist when their recruitment fluctuates asynchronously.

Apart from such hypotheses alleviating the impact of competition, it is hypothesized that many species coexist because the mobility of the individuals is restricted.

A model was constructed for evaluating life-history tactics, feeding guilds and adaptations of coexisting soil mites to their biotopes (Chapter 6). The model assumed logistic growth for fungi in each of 15,000 grids; the value of K of this function did not influence equilibrium population size of fungivorous mites. As food was limited in supply, competition occurred. Two identically defined species were competitors for two sets of runs. In both sets of runs, the species were initially completely mixed. Extinction occurred stochastically. According to the Lotka-Volterra model, in the first set of runs mobility was unlimited for both species: all grid cells could be reached at each time step by any individual (52 steps per generation). The mean chance of extinction of either species appeared to be once in 141 generations. Thus, for unrestricted mobility, the competitive exclusion principle indeed held. In the second set of runs, mobility was limited to adjacent grid cells at each time step. The mean chance of extinction of either species then was once in 66,086.712 generations, thus approaching an evolutionary time scale; differences between the two sets of runs were significant (F-test: $p < 0.001$). Species still were completely mixed and food was limited (Fig. 7.1). So, coexistence was infinite for restricted mobility of the individuals, *i.e.* the competitive exclusion principle did not apply. Therefore it is hypothesized that the less mobile individuals are, the less effective competitive exclusion between species becomes.

Is this model realistic? Thelytokously reproducing species are sufficiently similar to test the model as their asexual reproduction results in clone formation, clones differing only to an ecologically irrelevant degree. From the above hypothesis it is to be expected that formation of clones will be rarest in the most mobile species, and commonest in those with restricted mobility. This is exactly what is found: most thelytokously reproducing species are found among plants and invertebrates, and within those groups, they are the least mobile species. Thelytoky is more common

in flightless weevils and euedaphic springtails than in dragonflies and butterflies, more common in oribatid mites than in obligately phoretic mesostigmatid mites (Suomalainen, 1962, Chapter 2).

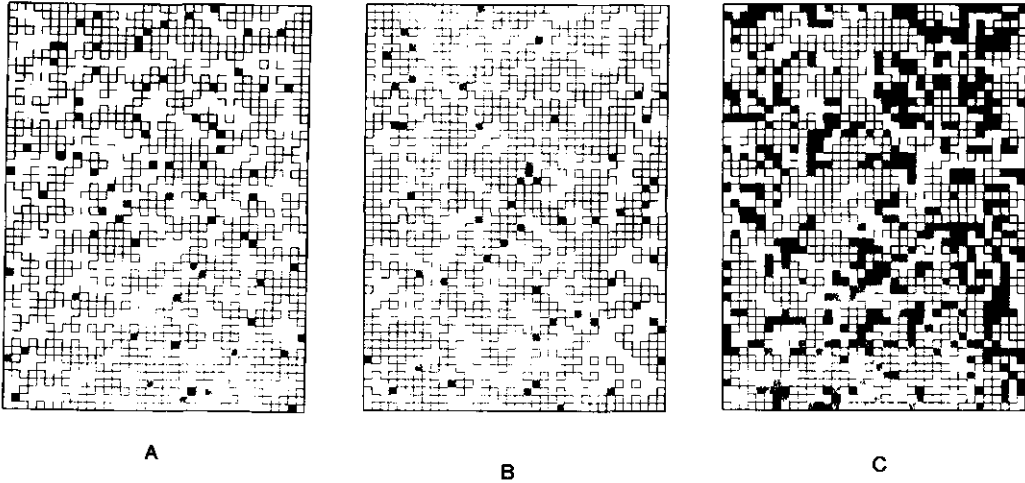


Figure 7.1. Distribution patterns of species 1 (A), species 2 (B) and food (C) over grid sections after 100 generations. Species were defined as being identical and their mobility was restricted per time-step to orthogonal neighbouring grid cells.

Speciation will be faster in less mobile than in very mobile species, the former lacking competitive exclusion. Stanley (1989) mentions ineffective dispersal as a promotion of speciation, but continues that this ineffective dispersal also increases rate of extinction. This last assumption may be questionable now. This means, therefore, that the balance between speciation and extinction is changed, or that a higher rate of extinction has other causes.

Recently, the distinction of local versus global movements (individual mobility!) also gave surprising results in parasitoid-host relationships: local movements stabilized Nicholson-Bailey models that were unstable per grid cell in arrays larger than 15 x 15 (Hassell *et al.* 1991).

Introducing restricted mobility of individuals as a parameter can result in a general theory of coexistence and local diversification of clones and species on both an ecological and an evolutionary time scale. This possibility should, therefore, be tested experimentally, and be formalized in equations on competition and predator-prey relationships.

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8

General discussion

A BRIEF OVERVIEW OF CURRENT APPROACHES

The majority of studies on soil microarthropod communities are inspired by the high numbers microarthropods reach in soil and the important role they are thought to play in nutrient cycling and soil fertility (*e.g.* Badejo & Lasebikan 1988, Hågvar 1988, Hågvar & Kjøndal 1981, Fager 1968, Ibarra *et al.* 1965, Lagerlöf & Andrén 1988, Petersen & Luxton 1982, Seastedt *et al.* 1989).

The most simple way of studying environmental and human-induced effects on microarthropod communities is to take soil samples, extract the microarthropods, count the numbers, either in total or by systematic groups, and repeat this after the measures to be studied are taken. In better experimental designs also repeatedly sampled unaffected control plots are included in the analysis. Examples of such studies are Abo-Korah *et al.* 1984, Badejo & Lasebikan 1988, Burghouts *et al.* 1992, Ehler & Frankie 1979, Gasdorf & Goodnight 1963, Holt 1981, Mallow *et al.* 1984, Plowman 1981a, b. A common feature of these studies is a lack of systematic detail. Although sometimes quite forcing reasons for this lack of detail exist, such as insufficient systematic knowledge or time shortage, the results of these studies are of limited use.

In many other community studies soil microarthropods are identified to the species level. In studies focussed on the community level usually the average reaction pattern of soil microarthropods on whatever factors are described, taking into account numbers, species diversity and changes in the species composition (*e.g.* Abbott *et al.* 1980, Aoki 1976, Athias-Binche 1983, Curry & Momen 1988, Hågvar & Amundsen 1981, Kaneko 1985, Lebrun 1965, Siepel & Van de Bund 1988, Zyromska-Rudzka 1979). Due to the enormous species diversity of soil microarthropods and the many different ways these

species are affected by human influences, it is often impossible to extract clear patterns from this amount of information. Moreover, the majority of this work is based on correlations and gives no grip on possible causal mechanisms. In studies focussed on the species level in the past decades much information on biotope conditions of particular species has been obtained. These studies contain many faunistic elements and may also serve well in future research for comparison of biotope data per species (e.g. André 1985, 1986, Bukva *et al.* 1976, Colloff 1983, 1988, Dalenius 1962, Engelmann 1972, Fujikawa 1970, 1975, Haarløv 1960, Hammer 1952, Huçu 1982, Karg 1986, Karppinen 1955, 1958, Knülle 1957, Luxton 1981a, b, c, d, Märkel 1958, 1964, Metz 1971, Mitchell 1979, Murphy & Jalil 1963, Norton 1983, Oswald & Minty 1970, 1971, Pande & Berthet 1975, Popp 1970, Poursin & Ponge 1984, Pugh & King 1988, Rajski 1970, Riha 1951, Schulte *et al.* 1975, Stamou & Sgardelis 1989, Weigmann & Kratz 1981, Wood 1967a, b).

Usher *et al.* (1982) stressed the importance to also study general natural history, life-history strategies and ecological physiology of individual species of microarthropods. Examples of such autecological studies are relatively few in soil microarthropods (e.g. André & Vöglin 1982, Athias-Binche 1977, 1981, 1982, Binns 1982, Butcher *et al.* 1971, Grandjean 1950, Lions & Gourbière 1988, Madge 1964, Mitchell 1979, Pan & Shimida 1991, Schulte 1974, Sømme 1981, Sømme & Conradi-Larssen 1977, Wallwork 1960, Wallwork *et al.* 1984, Young 1980). The value of these studies lies particularly in the fact that the species characteristics measured may be valid on every location, every time the species is found in a sample, which may step by step explain the local composition of the soil microarthropod communities. A common feature of species-oriented community studies, however, is that they result in much information per species, but little insight into the diversity and coexistence of soil microarthropods.

In this thesis species characteristics of soil microarthropods, either from literature data or from own experiments, were the starting point for explanation of reaction patterns in soil microarthropod communities. The structure of microarthropod communities, in both natural and disturbed biotopes and during the process of decomposition of organic matter, was elucidated by the classification of life-history tactics, based on well-defined traits (Chapters 2 & 3). The function of soil microarthropod communities was elucidated by assembling microarthropods in feeding guilds (Chapters 4 & 5). In a simulation model both life-history traits and feeding guilds were connected to investigate whether a relatively low degree of efficiency of food use could be compensated by a relatively high degree of adaptation in life-history traits, thus enabling more species to coexist than there are resources available (Chapters 6 & 7).

LIFE-HISTORY TACTICS

A multidimensional classification of twelve life-history tactics was developed based on well-defined life-history traits covering reproduction, oviposition, development, synchronization and dispersal (Chapter 2). Forms of reproduction were preferred in the classification above reproduction rates. The most wide-spread form, after sexual reproduction, turned out to be thelytoky (asexual reproduction, whereby females lay unfertilized eggs from which again females hatch). In this type of reproduction no change in genetic composition takes place; groups of individuals share the same genotype ('clones'). Constancy of the environment was hypothesized, and was found, to favour this type of reproduction. Constant biotopes such as forest soils, and the later stages in the decomposition process had a comparatively high fraction of thelytokously reproducing microarthropods (Chapter 3). Constancy of the environment could also be created by man-induced pollution. Persistent pollution indeed also led to a high fraction of thelytokously reproducing animals (Chapter 3). The basic assumption here is, that during the first pollution all species are affected (most animals die), but by chance, in a number of species, some part of the population appears to be resistant. Thelytokously reproducing animals then have an advantage over sexually reproducing ones, because a resistant female gives rise to resistant off-spring. Sexually reproducing species have the disadvantage of possible recombination of the resistant genotype; the resistant genome is not inherited as such by all off-spring. Besides that, asexually reproducing species generally show a higher rate of increase, because they produce more females.

Several forms of synchronization were classified, from overcoming a harsh season by a simple slow-down of life-processes, to obligate diapause with a physiological base (Chapter 2). Ecologically these traits could be regarded as adaptations to irregular, unpredictable conditions (for instance flooding) on one side to adaptations to regular, predictable conditions (for instance seasonality) on the other side. Regular disturbances led to an increase of species with well-developed synchronization tactics. *E.g.*, the annual filling up and the gradual draining of a barrage resulted in a regular disturbance at the borders; species at rest during flooding were very abundant (Chapter 3).

Traits for dispersal were grouped in directional migration (phoresy) and unidirectional movements (anemochory). Phoretic species (carrier-unspecific) were very dominant during the first stages of litter decomposition, and irregular unpredictable disturbances also led to an increase of phoretic species, again especially those with obligate carrier-inspecific phoresy (Chapter 3). Differentiation should be made between obligate and facultative

phoresy and between carrier-specific and carrier-inspecific phoresy. Contrarily to what usually is assumed (Binns 1982) phoresy appeared not to be a r-selected trait. Carrier-specific phoresy appeared to be K- or S-selected rather than r-selected.

In contrast to the multidimensional system of life-history tactics presented in Chapter 2, former classifications of life-history tactics (MacArthur & Wilson 1967, Greenslade 1983, Grime 1977, Holm 1988, Southwood 1977, Stearns 1976) did not permit practical use in applications in nature management or ecotoxicology, because definitions of those strategies were too general, at best allowing allocation of species with very distinct life histories to strategies (Chapter 3).

FEEDING GUILDS

Five major feeding guilds of mites were distinguished, based on gut carbohy-drase activities, in order to shed light on the function of microarthropods in soil (Chapter 4).

Cumulative microbial respiration (CO₂ production) from pulverized leaves of *Avenella (Deschampsia) flexuosa* was measured at regular intervals during microcosm experiments. The presence of herbivorous grazers resulted in neither an increased nor a decreased CO₂ production. The presence of fungivorous or herbofungivorous grazers resulted in an increased production of CO₂. The presence of fungivorous browsers or opportunistic herbofungivores resulted in a decrease of the CO₂ production. Thus digestion of fungal cell-walls (chitinase activity) by the (herbo-)fungivorous grazers resulted in an increased rate of decomposition. Chitin, an important component of the fungal cell-wall, contains about 7% N. Evidence was obtained that the digestion of fungal cell-walls resulted in the release of extra N, which stimulated microbial growth and respiration and thus increased the decomposition rate (Chapter 5). Hence, the type of food digestion of microarthropods helps to explain their function in soil.

COEXISTENCE

In chapter 6 and 7 the accumulated knowledge of the structure and function of soil microarthropod communities was used to shed light on the coexistence of species by a model including spatial heterogeneity of food and including mites with different efficiencies of use of food and different life-history tactics. It appeared that being tolerant for short-term en-

vironmental extremes, being able to bridge a long period without food or having a relatively high mobility might compensate for a less efficient use of food (digestion of cell-contents only instead of both cell-contents and cell-walls, i.e. browsers versus grazers). Species diversity could also be higher at low frequencies of disturbance, compared to no disturbance at all (exclusion of the inferior competitor), or a high frequency of disturbance (neither one of the species could persist) in agreement with the hypothesis of Huston (1979). Furthermore it appeared that more species than resources could be present without exclusion of one of the competing species. When two species were defined as having the same niche it appeared that when both species had an unlimited mobility either one of the species went extinct within about 140 generations, but when mobility of both species was limited (as it usually is), both species might coexist for more than 66,000,000 generations (Chapter 6). So competitive exclusion (Hardin 1960) may exist only by approximation in very mobile species, and is thus not a general ecological principle. In nature two species are never exactly alike, but the model shows that it is not necessary to assume that differences between species are a prerequisite for their joint existence (Chapter 7). The possible differentiation in food choice among soil microarthropods may be considerable, but can hardly explain their species diversity. Because the model shows that the lower the mobility in a group of species is, the less forcing is the principle of competitive exclusion, the question 'why are there so many species?' (Anderson 1975) should be replaced by 'why are there so few?'

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Summary

Resources in soil must be very numerous to explain the species richness with the hypervolume model, in which each species has its own niche, originating from selection for minimal niche-overlap. The objective of this thesis was to investigate whether a limited number of resources can support a high number of species. Species of the soil fauna, particularly microarthropods, were classified according to their life-history tactics and assembled in feeding guilds. In a simulation model the species with different life-history tactics and feeding guilds were included to investigate whether inefficient use of food may be compensated with other traits, such as high mobility, or tolerance for harsh conditions. The simulation model also made it possible to define two species having the same niche and to follow interspecific competition in time.

Microarthropod life-history tactics were based on well-defined traits in reproduction, oviposition, development, synchronization, and dispersal (Chapter 2). In *reproduction* more value was given to the type of reproduction than to reproductive capacity. Reproduction forms used in the definition of the tactics are: thelytoky, asexual reproduction with females only, arrhenotoky, asexual reproduction with males hatching from unfertilized eggs, and sexual reproduction. Also types of *oviposition* were used as traits: semelparity (all at once) and iteroparity (spreading in oviposition). The number of developmental stages is rather uniform within taxa, differences in *rate of development* among species within a taxon may be quite large. Within species, the rate of development may be influenced by food quality and temperature. Non-diapause dormancy, a short interruption of development, and real diapause dormancy during winter or summer are *synchronization* traits. Semelparity may also be included here as a synchronization trait. *Dispersal* is usually poorly developed in microarthropods; the walking range is often small. Ways to bridge longer distances are phoresy (hitch-hiking with bigger animals, mostly insects) or anemochory (moving by wind). Twelve life-history tactics were defined, ordered in tactics for synchronization, dispersal, or different types of reproduction. The classification of tactics was compared with former classifications. Projection of the tactics on MacArthur and Wilson's r-K continuum, the R-G-S triangle of Grime, the time-biotope quadrant of Southwood, and comparison with the classification of Stearns, showed that the tactics defined in this thesis are more differentiated. These tactics may be used for other taxa than microarthropods as well; the traits the tactics are based on occur in many groups of organisms.

Allocation of microarthropod species to the life-history tactics was made possible by a key, which made applications in natural and disturbed or polluted biotopes relatively easy (Chapter 3). More or less natural biotopes, such as the soil of a forest, a grassland, and a salt-marsh, and the process of decomposition of litter, could be characterized quite well in terms of representation by life-history tactics of soil microarthropods: in natural biotopes no high fractions of specialized tactics

were found, but mites with thelytokous reproduction increased in the sequence salt marsh - grassland - forest soil, whereas these mites in the later stages in the decomposition process also reached the highest fractions. The same good characterization held for disturbed soils: cattle-grazed grasslands had a high fraction of phoretic species, the bank of a barrage a high fraction of species with synchronization tactics, and sites with a permanent pollution (persistent pesticides, heavy metals) appeared to have high fractions of thelytokously reproducing species.

Feeding guilds were defined on the basis of carbohydrase activities (gut enzymes), particularly cellulase, chitinase, and trehalase (Chapter 4). Cellulase activity points to feeding on plant material, trehalase activity points to feeding on fungal cell-contents, and chitinase activity indicates that the fungal cell-wall can be digested. Species able to digest cell-contents only are called browsers. Species able to digest cell-walls as well are called grazers. Among the fifty species under study, five large species groups (herbivorous grazers, herbofungivorous grazers, fungivorous grazers, fungivorous browsers, and opportunistic herbo-fungivores) and two single species groups (a herbivorous browser and an omnivore) were recognized. The major difference with former classifications is, apart from the unequivocal definition, the distinction between fungivorous species digesting fungal contents only (browsers), and species digesting both cell-walls and cell-contents (grazers).

In order to examine whether feeding differences would indeed show differences in the decomposition of pulverized leaves, experiments were carried out with representatives of each of the feeding guilds (Chapter 5). In the presence of (herbo)fungivorous grazers a higher CO₂ evolution was measured than in their absence, as expected, while in the presence of fungivorous browsers, or opportunistic herbofungivores, a lower CO₂ evolution was measured than in their presence. Digestion capacity of the mites indeed appeared to be important for insight into their function in soil.

In a spatial simulation model the coexistence of the browsers, with their less efficient digestion of food, and the grazers with their more efficient digestion of food, was investigated (Chapter 6 & 7). A higher mobility, or a better tolerance for short-term environmental extremes, or a longer starvation period of browsers made them coexist with the more efficient users of food. A low frequency of disturbance led to coexistence of an efficient with an inefficient user of food; not the food but the disturbances limited population size in both species in such cases. In the simulations a higher number of species was found to be able to coexist than the number of resources that were present. Species with identical niches and traits could coexist for about 66 million generations, as long as their mobility was limited. When both species were defined with unlimited mobility, one of them went extinct in about 140 generations. The simulations, which included the best available knowledge on life-history tactics and feeding guilds, indicated that competitive exclusion will rarely occur among soil microarthropods, if at all. Hence, competitive exclusion is not a general ecological principle.

Samenvatting

De bronnen van bestaan in de bodem zouden zeer talrijk moeten zijn om de bestaande soortenrijkdom te verklaren op grond van het hypervolumemodel, waarin iedere soort een karakteristieke nis bezet en overlap met de nissen van andere soorten door selectie zoveel mogelijk beperkt is. In dit proefschrift wordt onderzocht of het werkelijk nodig is dat elke soort een unieke nis bezet, of dat er met een beperkt aantal bronnen van bestaan ook sprake kan zijn van grote soortenrijkdom. Een soortenrijke groep van bodemdieren, de microarthropoden, zijn in dit proefschrift ingedeeld in overlevingsstrategieën en voedselgildes. In een simulatiemodel, waarin soorten met verschillende overlevingsstrategieën en verschillende voedselgildes zijn opgenomen, wordt onderzocht of een inefficiënter voedselgebruik gecompenseerd kan worden met andere eigenschappen, zoals grotere mobiliteit of tolerantie voor ongunstige periodes. Het simulatiemodel bood ook de mogelijkheid twee soorten met precies dezelfde nis te definiëren en de concurrentie van de soorten door de tijd te volgen. Met behulp van de genoemde indelingen: in overlevingsstrategie, voedselgilde en tolerantie voor ongunstige periodes, konden verschillende aspecten van het leven in de bodem worden verhelderd.

De overlevingsstrategieën van de microarthropoden zijn gebaseerd op goed gedefiniëerde eigenschappen op het vlak van reproductie, ei-afzetting, ontwikkeling, synchronisatie en verbreiding (Hoofdstuk 2). Wat betreft reproductie is meer waarde gehecht aan de vormen van reproductie dan aan de reproductiecapaciteit. Vormen van reproductie die gebruikt zijn voor de definitie van de overlevingsstrategieën zijn: thelytokie, asexuele reproductie met alleen vrouwtjes, arrhenotokie, asexuele reproductie met mannetjes uit onbevuchte eieren, en sexuele reproductie. Ook vormen van ei-afzet in de tijd: semelpariteit (alles ineens) en iteropariteit (spreiding in de tijd) zijn als eigenschappen gebruikt. Aantallen ontwikkelingsstadia van de soorten zijn binnen taxa vrij uniform, maar verschillen in *ontwikkelingssnelheid* tussen soorten in eenzelfde taxon kunnen groot zijn. Binnen de soort kan de ontwikkelingssnelheid beïnvloed worden door voedselkwaliteit en temperatuur. *Synchronisatievormen* variëren van eenvoudige onderbrekingen van de ontwikkeling tot echte diapausevormen in winter of zomer. Semelpariteit kan ook als synchronisatievorm worden aangemerkt. *Dispersievormen* zijn bij microarthropoden vaak slecht ontwikkeld; het loopvermogen is doorgaans gering en de manier om grote afstanden te overbruggen is foresie (het meeliften met grotere dieren, meestal insecten) of anemochorie (windverbreiding). Twaalf overlevingsstrategieën zijn gedefiniëerd, gegroepeerd in strategieën gericht op synchronisatie, verbreiding, of verschillende reproductievormen. Deze strategieën worden vergeleken met eerdere indelingen. Projectie van de strategieën op het r-K continuum van MacArthur en Wilson, in de R-C-S driehoek van Grime, in het tijd-biotop kwadrant van Southwood, en vergelijking met de indeling van Stearns, laat zien dat de hier gedefiniëerde strategieën beter gedifferentieerd zijn. De strategieën kunnen, behalve bij microarthropoden, ook bij andere levensvormen worden gebruikt; de eigenschappen waarmee ze zijn gedefiniëerd komen in allerlei groepen van organismen voor.

Voor de indeling van soorten microarthropoden in overlevingsstrategieën werd een sleutel ontwikkeld, waardoor toepassing van de indeling in natuurlijke en verontreinigde biotopen betrekkelijk eenvoudig is (Hoofdstuk 3). In min of meer natuurlijke biotopen, zoals de bodem van een bos, een grasland en een kwelder, en gedurende het afbraakproces van bladstrooisel, zijn milieucondities en afbraakstadia goed met de gedefiniëerde strategieën te karakteriseren: thelytoke reproductie heeft een relatief toenemend aandeel in de reeks kwelder - grasland - bosbodem; in de latere stadia van het afbraakproces is thelytoke reproductie de meest algemene strategie. Voor storingssituaties blijkt de goede karakterisering ook te gelden: begraaide graslanden hebben een relatief groot aandeel foretische soorten, de oeverzone van een stuwmeer heeft een groot aandeel soorten met synchronisatiestrategieën en gebieden met een blijvende verontreiniging (persistente pesticiden, zware metalen) blijken een groot aandeel soorten met thelytoke voortplanting te herbergen.

Voedselgildes zijn gedefiniëerd op basis van activiteiten van enkele verteringsenzymen uit het maag-darmkanaal, namelijk cellulase, chitinase en trehalase (Hoofdstuk 4). Cellulase-activiteit duidt op eten van plantaardig materiaal, trehalase-activiteit duidt op eten van schimmelcelinhouden en chitinase-activiteit geeft aan dat de schimmelcelwand kan worden verteerd. Soorten die alleen celinhouden kunnen verteren worden browsers genoemd. Soorten die ook de celwand kunnen verteren worden grazers genoemd. Onderscheiden zijn: herbivore grazers, herbofungivore grazers, fungivore grazers, fungivore browsers en opportunistische herbofungivoren (elk met verscheidene soorten mosmijten) en herbivore browsers en omnivoren (met elk één soort mosmijt uit de vijftig onderzochte soorten). Het belangrijkste verschil met vroeger gebruikte classificaties is de eenduidige definitie en het onderscheid tussen soorten die de schimmels slechts ten dele kunnen verteren (browsers) en soorten die de schimmels vrijwel geheel kunnen verteren (grazers).

Om te onderzoeken of dit laatste onderscheid verschillen te zien zou geven in de afbraak van verpulverd blad door schimmels, zijn met vertegenwoordigers van elk van de gildes decompositie-experimenten uitgevoerd (Hoofdstuk 5). Zoals verwacht bleek in aanwezigheid van (herbo)fungivore grazers een grotere microbiële CO₂-productie gemeten te worden dan in hun afwezigheid, terwijl in aanwezigheid van fungivore browsers of opportunistische herbofungivoren juist een lagere CO₂-productie werd gemeten dan in hun aanwezigheid. De verteringscapaciteit van schimmel-etende mijten blijkt dus van invloed te zijn.

Met behulp van een simulatiemodel werd onderzocht of de minder efficiënte voedselvertering van browsers vergeleken met die van grazers door andere eigenschappen zodanig kan worden gecompenseerd, dat coëxistentie van meer soorten dan bestaansbronnen mogelijk is (Hoofdstukken 6 en 7). Een grotere *mobilititeit* van browsers kan ze in staat stellen toch in aanwezigheid van de betere voedselconcurrent te overleven, evenals het *tolereren van korte, onverwachte, ongunstige omstandigheden*, of het *langer zonder voedsel kunnen*. Een lage frequentie van verstoringen blijkt tot coëxistentie van een soort met een inefficiënt voedselgebruik met een

soort met een efficiënter voedselgebruik te kunnen leiden; niet voedsel, maar de verstoringsfrequentie limiteert de populaties in zulke gevallen. Er blijken meer soorten samen voor te kunnen komen dan het aantal gedefiniëerde voedselbronnen. Soorten met een identieke nis en eigenschappen kunnen naast elkaar blijven voortbestaan (gemiddeld 66 miljoen generaties) zolang hun mobiliteit niet onbeperkt is. Geldt voor beide soorten geen beperking in hun mobiliteit dan sterft een van beide soorten binnen gemiddeld 140 generaties uit. Uit de simulaties, gebruik makend van de beschikbare kennis op het gebied van overlevingsstrategieën en voedselgildes, blijkt dat uitsluiting door concurrentie bij bodemmicroarthropoden maar in zeer weinig gevallen een rol zal spelen, als het al zou bestaan. Uitsluiting door concurrentie is dus geen algemeen oecologisch principe.

Curriculum vitae

Henk Siepel werd geboren op 31 juli 1959 te Ede. In 1977 behaalde hij het diploma Ongeedeeld V.W.O. aan het Christelijk Lyceum te Veenendaal. Daarna studeerde hij biologie aan de Rijksuniversiteit Utrecht, waar hij in 1980 het kandidaatsexamen aflegde. In 1984 studeerde hij af (cum laude) met als hoofdvakken Vegetatiekunde/Botanische Oecologie en Zoölogische Oecologie en als bijvak Bodemkunde. Tijdens de doctoraalfase van zijn studie werkte hij als studentassistent bij de vakgroep Zoölogische Oecologie en Taxonomie, de vakgroep Vegetatiekunde en Botanische Oecologie en de vakgroep Petrologie, Mineralogie, Kristallografie, Geochemie en Bodemkunde. In 1984 trad hij in dienst als toegevoegd onderzoeker bij de vakgroep Zoölogische Oecologie en Taxonomie van de Rijksuniversiteit Utrecht. Eind 1984 kwam hij als onderzoeker evertrebraten in dienst bij het toenmalige Rijksinstituut voor Natuurbeheer, nu DLO-Instituut voor Bos- en Natuuronderzoek. In 1993 is hij daar benoemd als projectgroepleider herpetologie, entomologie en meetnetontwikkeling in de afdeling Dierecologie.