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The role of soil predators in decomposition processes

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Abstract. There is a limited number of papers which deal with the significance of predation in the decomposer food chain. Microcosm experiments conducted in order to examine the role of predatory microfauna (Protozoa, Nematoda) showed that they increase the rate of decomposition of organic material and enhance the mineralization rate of nitrogen and phosphorus.

Experimental results on the importance of larger predators, belonging to the meso- and macrofauna (Acarina, Araneae, Carabidae, Formicidae) were less consistent. In most cases it was found that they can retard the process of organic matter decomposition and contribute to system stabilization. However, in some experiments their effect on the decomposition rate was negligible.

Data concerning food composition of spiders show that these animals can be included both in the grazing and detrital food chains. It is likely that assemblages of spiders can affect decomposition processes.

INTRODUCTION

The hypothesis that spiders can limit herbivore populations, especially insect pests, has been tested by many authors (Kiritani & Kakiya, 1975; Mansour et al., 1980; Riechert, 1974; Riechert & Bishop, 1990; Wise, 1993). However, the diet of spiders consists not only of herbivores but also of saprophages, microphytophages and predators. Predation on animals representing the detrital food web occurs not only among soil dwelling spiders but at least partially also among those hunting above ground.

It can be assumed that spiders which feed on decomposers not only affect the prey population but also indirectly influence the processes of matter decomposition.

The aim of this article is to demonstrate, using literature data, that spiders can be included in the detritus based food chain and to analyse the role of predation in the soil.

THE MAIN DIET OF SPIDERS

The insects trapped by spiders are mainly Diptera. In the webs of orb weavers, Diptera make up about 40 to over 90% of all the prey caught, depending on the species of spider and its habitat (Table 1). The percentage of these insects caught by space web building spiders (Linyphiidae) is significantly less, 6 to 40% (Table 2). Diptera represent 25 to 32% in the diet of epigean wolf spiders (Lycosidae) (Table 3) but reach up to 67% in females of *Pardosa amentata* (Edgar, 1970b). Dipterans belong to various trophic catagories, but are mostly detritophagous or herbivorous.

Based on a limited number of papers (Turnbull, 1960, 1966; Kajak, 1965; Nentwig, 1983), where Dipterans were identified to the family level, it was possible to assume that, at least in seminatural grasslands and wetlands, detritophages predominated among dipterans which were captured in webs. The dominant families were Chironomidae and

TABLE 1. Prey composition (%) of orb-weaving spiders (Araneidae, Tetragnathidae) in grasslands and cultivated fields.

Prey	Seminatural grasslands and wetlands			Managed grasslands	Cultivated fields	Main trophic category of prey*	Author
	Araneus spp.	*Larinioides cornutus*	Various species	*Larinioides cornutus*	Various species		
Diptera	57.1–88.2	75.4–85.1	41.6–89.8	83.5–96.0	68.8–92.1	D, H	Nyffeler, 1982
	59.5–78.9	38.2–81.9					Kajak, 1965
	78.8	70.9					Nentwig, 1983
Chironomidae	4.0–23.5	8.5–75.8				D	Kajak, 1965
	70.9	51.6					Nentwig, 1983
Sciaridae	16.6–31.4	0.4–27.7				D	Kajak, 1965
Cecidomyiidae	2.2	11.5				H	Nentwig, 1983
Aphidoidea	1.8–13.0	4.2–12.2	0–18.6	0.9–2.4		H	Nyffeler, 1982
	3.1–13.0	7.1–14.6					Kajak, 1965
	16.2	13.7					Nentwig, 1983

* D – detritophages; H – herbivores

TABLE 2. Prey composition (%) of space web spiders (Linyphiidae) in grasslands and cultivated fields (After: A – Nentwig, 1983; B – Wingerden, 1975; C – Nyffeler, 1982; D – Nyffeler & Benz, 1988a; E – Sunderland et al., 1986).

Prey	Seminatural grasslands		Managed grasslands		Cultivated fields		Trophic category*
	A	B	A	C	D	E	
Diptera	40.2		15.8	7.3	13.5	5.6	
Chironomidae	35.5		9.6				D
Aphidoidea	37.5		62.7	26.1	38.7	12.1	H
Collembola	2.0	main prey	0.2	45.4	37.8	71.7	M

* D – detritophages; H – herbivores; M – microphytophages.

TABLE 3. Prey composition (%) of wolf spiders (*Pardosa* spp., Lycosidae). (After: A – Nentwig, 1986 (Literature review); B – Edgar, 1970a,b; C – Nyffeler, 1982; D – Nyffeler & Benz, 1988b).

Prey	A	B	C	D
Diptera	32.0	32.0–67.0	12.0–26.0	15.7
Aphidoidea	4.8	0.0– 2.0	20.0–24.0	15.4
Collembola	20.8	2.0–13.0	2.0–40.0	13.5
Araneae	24.5	11.0–24.0	2.0–16.0	3.7

Sciaridae, insects whose larval stages feed on dead organic matter.

The second very important group of prey consists of Aphidoidea. They are all herbivorous. Their feeding habits significantly influence soil processes (Chmielewski, 1995; Andrzejewska, 1995). As sucking insects they are able to modify the water content of plants and of the soil, and by excreting sugar-rich honeydew stimulate microbial development.

Collembola are the next important group of prey.

They are most commonly micromycophages and are an important food component of spiders that build webs on the ground and those wandering on the soil surface, for example Linyphiidae (Table 2) and Lycosidae (Table 3). In some cases Collembola constitute up to 72% of the prey caught (Table 2).

In the diet of certain spider species, predatory animals form an important component, especially spiders and less commonly ants.

Turnbull (1966) analysed the trophic categories of spiders'prey in an over-grazed pasture. Detritophages and microphytophages were found to make up 38% of the food, and in the papers quoted earlier this percentage was even greater. Obviously, spiders prey upon different trophic groups and detritus based components form an essential part of their diet.

PREDATION AND DECOMPOSITION OF ORGANIC MATTER

Studies on the grazing food chain show that the numbers of herbivorous insects are often limited by predators which consequently decrease the damage to plants caused by noxious insects (Huffaker & Messenger, 1976; Mansour et al., 1980; Murdoch et al., 1985; Chiverton, 1986; Riechert & Bishop, 1990). The role of predation in the detritus food chain is difficult to estimate and not fully understood.

TABLE 4. Effect of predation on number of microphytophages and decomposition rate (After: Santos et al., 1981; Santos & Whitford, 1981; Elkins & Whitford, 1982; Werner & Dindal, 1987; Moore et al., 1988; Walter et al., 1988; Setala, 1990; Setala et al., 1991; De Ruiter et al., 1993; Bouwman et al., 1994).

Response	Number of analysed papers	
	Prey density	Litter disappearance and matter mineralization rate
Increased	0	9
No response	0	0
Decreased	5	1
Regulation	1	0

PREDATORY MICROFAUNA

During the last few decades, microcosm experiments have been developed to study interactions among populations and to simulate soil processes. Most frequently, such experiments have been carried out in small containers with soil and litter taken from the field. The soil was sterilized, then specific groups of organisms were reintroduced.

The changes in the number and biomass of organisms and in the amount of nutrients released by their metabolism were recorded. Most commonly carbon, nitrogen and phosphorus were analysed. These studies mostly served to explain the influence of microbial grazers on litter mineralization. In some cases the role of zoophages was also included. Because of the small surface area of microcosms, most frequently very small predators (microfauna) were used in such experiments.

The results of experiments estimating the influence of predatory microfauna are very consistent: the density of microphytophages decreased in treatments where predators were present, but the rate of decomposition and respiratory activity was significantly raised (Table 4). The experimental findings are explained by the fact that a lack of predation results in overgrazing the microflora by microphytophages and thus reduces decomposition rate.

PREDATORY MESO- AND MACROFAUNA

An increasing number of experiments have been carried out in larger areas (a few hundred cm^2) than microcosms, the so-called meso- and macrocosms, with more spatial heterogeneity and complex biota (Setala, 1990). Another method of analysis has been the application of biocides which remove selected groups of organisms (Santos & Whitford, 1981; Parker et al., 1984). However, experiments analysing the role of larger invertebrate predators belonging to the meso- and macrofauna connected with the detritus food chain have rarely been carried out.

The large predators found in the soil and ground litter are often polyphagous. Most abundant among them are predatory mites (Acarina), spiders (Araneae), ants (Formicidae) and ground beetles (Carabidae). A series of very good and interesting field experiments has been conducted on assemblages of these large polyphagous predators. Spiders dwelling on the soil surface have also been included in the analysis.

However, only their influence on numbers of herbivores and their role in plant protection has been analysed (Chiverton, 1986; Gravesen & Toft, 1987; Riechert & Bishop,

TABLE 5. Effect of predatory meso- and macrofauna on prey number and decomposition rate of organic mater (Based on: Clarke & Grant, 1968; Kajak & Jakubczyk, 1975; Breymeyer, 1978, 1981; Kaczmarek, 1978; Santos & Whitford, 1981; Martikainen & Huhta, 1990; Setala, 1990; Kajak et al., 1991; Gunn & Cherrett, 1993; Brussard et al., 1995; Laakso et al., 1995).

Response	Number of analysed papers	
	Prey density	Decomposition rate and N release
Increased	0	0
No response	1	4
Decreased	8	6
Regulation	2	2

1990; Thomas et al., 1991; Rodenhouse et al., 1992). These types of experiments were conducted on relatively large plots (several to several dozens of square metres). Barriers placed around them prevent the immigration of predators. In addition target groups were removed within fenced areas by pitfall traps or hand collection. In control plots the number of predators was enhanced by suitable conditions (e.g. by mulching or by perennial vegetation) (Nentwig, 1988; Riechert & Bishop, 1990). The advantage of these experiments is that they were conducted under undisturbed environmental conditions.

The experimental results on the role of large predators (meso- and macrofauna) in the detrital food chain were much more divergent than microcosm experiments with predatory microfauna. In most cases a decrease in prey density and retardation in decomposition rate was found. It is interesting to note that in no case was the decomposition rate accelerated. In several experiments the effect of predation on the decomposition rate was negligible, but only in one case (Gunn & Cherrett, 1993) was no effect on prey density recorded (Table 5).

The latter was a study in which the numbers of animals as well as feeding activity in the soil were estimated by field observations in rhizotrones instead of by various sampling methods. Linyphiid spiders were one of the analyzed predatory groups (Gunn & Cherrett, 1993). In the observations, only a 10 fold magnification was used. Therefore, very small animals and early stages of larger ones were excluded from the analysis. Most soil animals spend at least part of their life in the litter layer. This layer was excluded from this analysis, but it is intensely penetrated by predators both in forest ecosystems and in meadows (Kajak et al., 1971). Therefore, it is most likely that the litter layer is a predation arena for soil animals.

There may be various reasons for inconsistent experimental results relating to larger predators. One important reason may be the more complex system with multiple interactions compared with oversimplified microcosms. These diversified systems more closely reflect the system that exists in nature.

A series of studies have shown experimentally (Kaczmarek, 1961; Santos et al., 1981; Usher, 1985; Riechert & Bishop, 1990; Setala, 1990) or support the view (Breymeyer, 1981; Ingham et al., 1985; Moore et al., 1988) that predators, primarily assemblages of polyphagous predators, fulfil the role of stabilizing and regulating the ecosystem.

It was found that in treatments where predators were present, the litter decomposition rate was less dependent on changing environmental conditions (Santos & Whitford, 1981;

Santos et al., 1981). In more complicated systems, with at least three trophic levels, nutrients were more effectively utilized (Setala, 1990).

Most of the studies on predation have been done in herbivore-based food chains. It can be suggested that predation in decomposer-based food chains is of similar importance. Regulation and stabilisation of numbers and processes due to predation have also been found in grazing (Holling, 1959; Riechert, 1974) and in detritus food chains (Kaczmarek, 1961; Santos & Whitford, 1981; Ingham et al., 1985; Moore et al., 1988; Setala, 1990).

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