

Reactions to soil acidification in microarthropods: Is competition a key factor? *

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Summary. Acidification of raw humus soil in coniferous forest areas leads to characteristic changes in the microarthropod community. Certain species are “calciophilic” and decrease in abundance, while others are “acidophilic” and increase in abundance. The simplest explanation for these changes is that population levels are directly related to soil pH. This hypothesis was tested by growing small populations of selected species in monoculture at different pH levels. Three acidophilic species were tested, the collembolan *Mesaphorura yosii*, the oribatid mite *Nothrus silvestris*, and the astigmatid mite *Schwiebea* cf. *lebruni*. A slightly calciophilic collembolan, *Isotomiella minor*, was also included. For all species, population growth was lowest in acidified raw humus. Even acidophilic species seem to have an optimum at a high pH. It is assumed that their success in low-pH soils is due to their ability to compete under these conditions. Competition may be a key factor in microarthropod reactions to soil acidification.

Key words: Acid rain – Soil acidification – Microarthropods – Competition – Springtails – Collembola

The effect of soil acidification on microarthropods has been studied in the field using artificial acid rain, and in the laboratory by manipulating soil pH (reviews by Hågvar 1984c, 1987a). Liming was also carried out in several of these experiments. Certain species can be characterized as acidophilic, and others as calciophilic. Several hypotheses to explain these reactions have been discussed by Hågvar (1984c, 1987b,c, 1988a). Although many were refuted (especially Hågvar 1987b), competition appeared to be a possible key factor.

The present study, which examined the competition factor in pH reactions in more detail, was designed to test the hypothesis that the population growth of certain

microarthropod species can be directly correlated with soil acidity. This is the simplest way of explaining different population levels at different pH values. The hypothesis was tested by growing small populations of certain species as monocultures in soil adjusted to different pH levels.

Three acidophilic species were selected, the astigmatid mite *Schwiebea* cf. *lebruni* Fain, the oribatid mite *Nothrus silvestris* Nicolet, and the collembolan *Mesaphorura* (or *Tullbergia*) *yosii* Rusek. The collembolan *Isotomiella minor* (Schäffer) was included as a slightly calciophilic species. Several earlier experiments, as well as field studies in natural soils, have confirmed the characteristic relationships of these species to soil pH (Hågvar and Abrahamsen 1980; Hågvar and Amundsen 1981; Hågvar and Kjøndal 1981; Huhta et al. 1983; Hågvar 1984a, b; Hågvar and Abrahamsen 1984; Koskenniemi and Huhta 1986; Vilkkamaa and Huhta 1986). In earlier works by Hågvar, *Schwiebea* cf. *lebruni* has been referred to as *S.* cf. *nova* (Oudemans).

Materials and methods

The monocultures, which were started with 30 animals of *S.* cf. *lebruni* and 20 animals of the other species, were kept in small microcosms as described by Hågvar (1988b). Each microcosm contained about 2.3 g (dry mass) of mixed raw humus from spruce [*Picea abies* (L.) Karst.] forest. The pH was adjusted to three levels by treatment with H₂SO₄, distilled water, or Ca(OH)₂, according to Hågvar and Abrahamsen (1980). Before the animals were added manually from parent cultures, soil sterilization and reinoculation of microflora were undertaken as explained by Hågvar (1988b).

Samples were taken after 3, 6, and 12 months. Each time, samples of animals of each species were extracted from 11–16 microcosms (most often 14–15) at each pH level, so that the population growth could be described at different pH values.

Parallel to this work, a full microarthropod fauna was added to a number of microcosms by direct extraction from raw humus samples of corresponding volume. Since the extracted animals were allowed to fall directly into the microcosm, certain enchytraeids [*Cognettia sphagnetorum* (Vejdovsky)] were also introduced. These microcosms with a “full fauna” were included in the experiment to see if the pH re-

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actions observed earlier for each species would be repeated in a microcosm situation. If a species showed different reactions to soil pH in a monoculture compared to a community, this would indicate that other species affected the reaction pattern. The "full fauna" cultures were also sampled after 3, 6, and 12 months, with 21–26 microcosms sampled each time.

The microcosms were stored in the dark at 15 °C and approximately 80% relative humidity. Distilled water was added at intervals to maintain the original moisture level.

Results

Table 1 gives the pH values of the raw humus from the different samplings. In cultures of *Schwiebia cf. lebruni* and *Isotomiella minor*, the pH levels of the three chemical treatments remained distinct throughout the year. The same was true of *Nothrus silvestris* monocultures in the only samples taken after 1 year. In *Mesaphorura yosii* cultures, and especially in the "full fauna" cultures, the pH in limed raw humus fell towards the end of the year. The fall was so pronounced in the microcosms with a "full fauna" that the limed samples eventually reached the lowest pH.

Figure 1 shows the population changes for each species during the experimental period, both in the monoculture and in the "full fauna" situation. While *Mesaphorura yosii* needed a long time to build up a high population density in the monoculture, maximum populations of *Schwiebia cf. lebruni* and *Isotomiella minor* were recorded after 6 months. All three species reached very high numbers. It is not known whether a population peak for *Nothrus silvestris* occurred before the 12-month sampling. The monoculture data from all species, "acidophilic" or not, indicate that population growth was slowest in acidified soil. After 12 months, differences between populations in the acidified soil and the other treatments were significant in the first three species shown in Fig. 1, and in *Isotomiella minor* also after 6

months ($P < 0.05$). In the only monoculture sample taken of *Nothrus silvestris* (after 12 months), the difference between the acidified and the distilled water-treated soil was almost significant ($P \approx 0.06$).

Schwiebia cf. lebruni confirmed its acidophilic reaction after 6 months in a "full fauna" situation, with significantly higher populations in acidified soil ($P < 0.025$). A similar, but non-significant reaction appeared at a late stage with *Mesaphorura yosii*, but the situation was more obscure, since the limed raw humus in the "full fauna" became more acid than the other treatments at some point between 6 and 12 months from the beginning of the experiment (Table 1). The low abundance of *Isotomiella minor* in acidified raw humus together with a full fauna also confirmed its earlier characteristic as a slightly calciophilic species. The acidified soil supported significantly lower populations than the two other treatments throughout the study, except the limed soil after 12 months ($P < 0.05$). *Nothrus silvestris* surprisingly behaved like a non-acidophilic species in the "full fauna" situation. After both 6 and 12 months, populations were lowest in acidified soil ($P < 0.05$). The reaction of *Nothrus silvestris* may reflect the artificial conditions; there may have been too little space for this large species when it lived together with the full community. Its population fell markedly during the experimental period, and in the acidified microcosms, it eventually disappeared.

Discussion

The most important part of this experiment is the population growth of monocultures at different pH levels, since the acidophilic or calciophilic character of each species used has been well documented in earlier experiments with artificial acid rain and liming (Hågvar and Abrahamsen 1980; Hågvar and Amundsen 1981; Hågvar and Kjøndal 1981; Hågvar 1984a). The present study clearly shows that the population level (or population growth) of acidophilic species is not a simple function of soil pH, but may be modified by other factors, like the presence of other species. The hypothesis presented in the Introduction can thus be refuted.

On this basis, the following alternative hypothesis is presented: Certain acidophilic microarthropods express a preference for high pH values in monoculture by increased population growth. Their acidophilic character appears only in the presence of the whole soil community. This could reflect a better ability to compete at a low than at a high pH.

The great success of the relevant species at low soil pH is shown not only by the acidification experiments, but also by their occurrence in various natural soils of differing pH. *Schwiebia cf. lebruni*, *Mesaphorura yosii*, and *Nothrus silvestris* are all rare in high-pH soils, while they are often very numerous in low-pH soils (Hågvar 1982; Hågvar 1984b; Hågvar and Abrahamsen 1984).

In the acidification experiments referred to, the field plots contained a rather acid raw humus at the start, with high natural populations of the three species mentioned above. The finding that already dominant species were in-

Table 1. Raw humus pH ($\bar{x} \pm SD$) at time of sampling of microcosms, either with a "full fauna" or with monocultures of selected species

		Sampling I (3 months)	Sampling II (6 months)	Sampling III (12 months)
Full fauna of microarthropods	A	4.25 ± 0.10	4.33 ± 0.09	4.58 ± 0.10
	D	4.71 ± 0.08	4.72 ± 0.12	4.74 ± 0.27
	L	4.83 ± 0.10	4.45 ± 0.20	4.15 ± 0.16
<i>Schwiebia cf. lebruni</i>	A	4.05 ± 0.15	4.09 ± 0.10	4.27 ± 0.08
	D	4.61 ± 0.06	4.58 ± 0.09	4.56 ± 0.05
	L	4.85 ± 0.14	4.69 ± 0.09	4.88 ± 0.09
<i>Mesaphorura yosii</i>	A	3.83 ± 0.13	3.88 ± 0.11	4.28 ± 0.15
	D	4.50 ± 0.08	4.48 ± 0.08	4.81 ± 0.14
	L	4.79 ± 0.08	4.74 ± 0.11	4.55 ± 0.24
<i>Isotomiella minor</i>	A	4.13 ± 0.09	4.13 ± 0.10	4.49 ± 0.09
	D	4.57 ± 0.08	4.57 ± 0.07	4.82 ± 0.11
	L	4.78 ± 0.09	4.74 ± 0.13	5.08 ± 0.07
<i>Nothrus silvestris</i>	A			4.20 ± 0.13
	D			4.55 ± 0.24
	L			4.67 ± 0.23

A, acidified; D, distilled water-treated; L, limed. At the start, mean pH values were A: 3.36, D: 4.37, and L: 5.16

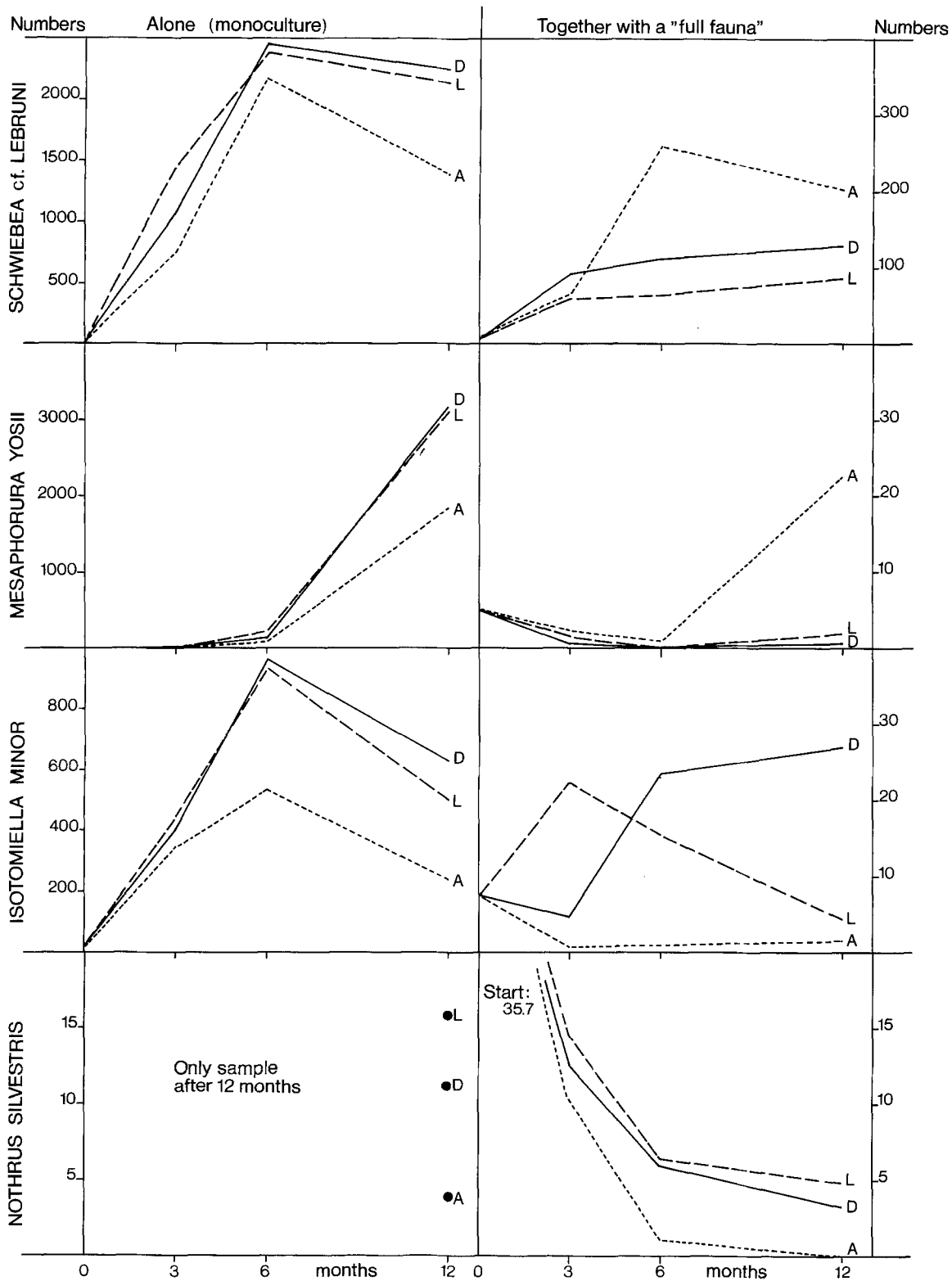


Fig. 1. Population changes in selected microarthropods at different soil acidity levels; A, acidified soil; D, distilled water-treated soil; L, limed soil; left: in monoculture; right: together with a "full fauna"

creasingly favoured as the pH declined, supports the view that their competitive ability increases with increasing acidity.

The hypothesis can be formulated more concisely: Competition is an important population-regulating fac-

tor for microarthropods; different pH levels favour different species in the competition process.

Competition is a wide concept, which includes many possible mechanisms. Little is known about competition between microarthropods, but certain studies have shown

that a species can be influenced by the presence of other, non-predacious species. Christiansen (1967) studied the effect of interspecific competition on the growth of collembolan populations in standard culture jars with excess food. Using 11 species in 13 interspecific interactions, he most often observed that one species was clearly dominant. The losing species was either prevented from reproducing or was quickly eliminated once reproduction had started. In four cases, one species was initially dominant but was gradually replaced by the second species. Only in one case was no dominance displayed, and the two species appeared to be able to coexist over time. The author concluded that the mechanisms differed with the interaction, with oviposition interference being the most common mechanism.

Nygaard and Solberg (1985) also studied the population growth of collembolan species in pairs versus monocultures, using the same microcosm type as in the present study. They found that the presence of another species always reduced population growth.

Among oribatid mites, Anderson (1978) showed that the vertical distribution of one species in a microcosm monoculture was affected by the addition of another species.

The acidophilic species in question (*Schwiebia* cf. *lebruni*, *Mesaphorura yosii*, and *Nothrus silvestris*) differ greatly in their ecology, including feeding habits. Yet they are similar in that they survive well at a low soil pH. The mechanisms behind this ability may be different for each species. Competition in particular forms may turn out to be an important factor in regulating the structure of soil animal communities.

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