Why do collemboles and mites react to changes in soil acidity?

SIGMUND HÅGVAR

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Artificial changes in the soil acidity (pH) by simulated acid rain, or by liming, affected the population size of many soil-living collemboles and mites. The results were supported by a laboratory experiment where the species were allowed to colonize sterile soil samples which had been adjusted to different pH levels. Certain species can be considered to be »acidophilic«, others »calciophilic«. These trends were also reflected through the abundance in various natural soils of different pH. Several hypotheses to explain these observations are discussed. Certain observations indicate that competition may be important. The present hypothesis is that at different soil pH levels, different species are favoured in the competition process.

S. Hågvar, Norwegian Forest Research Institute, Box 61, N-1432 Ås-NLH, Norway.

Introduction

Acid rain is a growing problem both in Europe and North America (Dovland et al. 1976, Anon. 1977, Likens et al. 1979), and possible effects of acidification on soil organisms have achieved increased attention. During the last ten years, field and laboratory studies in Norway have revealed that soil acidity (pH) is an important factor for several soil animals. The present paper will briefly refer the main conclusions concerning two very abundant groups: springtails (Collembola) and mites (Acari). Then, a number of hypotheses will be discussed for the explanation of the results.

Material and methods

Several field experiments were performed where experimental plots in coniferous forest were either limed or treated with artificial acid rain (Hågvar & Amundsen 1981, Hågvar & Kjøndal 1981, Hågvar 1984a). The results were in accordance with a »colonization experiment« where soil animals were allowed to colonize sterile soil samples which had been adjusted to different pH levels (Hågvar & Abrahamsen 1980). An important control of these two approaches was to study the occurrence of certain species in natural soils of different pH. If the abundance of a species was generally related to soil pH, this should also be reflected under natural field conditions (Hågvar & Abrahamsen 1984, Hågvar 1984b).

Results

When the treatments were strong enough to change soil pH, the abundance was affected in a great number of species. About 50 taxa could be sorted into four categories: 1. Increased abundance by acidification and/or reduced abundance by liming (»acidophilic« species); 2. Reduced abundance by acidification and/or increased abundance by liming (»calciophilic« species); 3. Reduced abundance recorded both by acidification and liming; 4. Various other reactions. A total survey of the reactions is found in Hågvar (1984c) and Hågvar (in press). The study of selected species in natural soils confirmed their relationships between abundance and soil pH. The main results were also supported by certain other Nordic studies (e.g., Bååth et al. 1980, Huhta et al. 1983).

Certain sensitive species should be mentioned. The most sensitive »acidophilic« species were three oribatid mites: *Tectocepheus velatus, Nothrus silvestris* and *Brachychochthonius zelawaiensis*, one astigmatid mite: *Schwiebea cf. nova*, and three collemboles: *Tullbergia (Mesaphorura) yosii, Anurida pygmaea* and *Willemia anophthalma.* A characteristic »calciophilic« species was the collembolan *Isotoma notabilis.*

Hypotheses

The most interesting part of this study is to try to explain the reactions. A number of hypotheses can be put forward which are worth discussing. Efforts have been made to refute them. The combination of field- and laboratory studies, and natural versus manipulated soil, makes it possible to refute at least some of the hypotheses. Since microarthropods have a water-repellent body surface, direct physiological effects are not considered here. The following set of hypotheses was discussed in the introduction to a doctoral thesis (Hågvar 1984c), but has not earlier been presented in a journal.

Hypothesis 1

The changes in the microarthropod fauna in the field experiments were indirectly due to the marked reduction of the ground vegetation (mainly the mosses) by the strongest treatments with sulphuric acid.

Comments: Similar changes in the microarthropod fauna were observed in experiments where the treated samples lacked vegetation during the whole experiment (Hågvar & Abrahamsen 1980, Hågvar & Kjøndal 1981). A special analysis of the abundance of the mite *Parazercon sarekensis* in one field experiment showed a distribution independent of the moss cover at each treatment (Hågvar & Amundsen 1981). The hypothesis can be refuted.

Hypothesis 2

The faunal changes in the liming and acidification experiments were not due to the soil pH changes as such, but more directly to the lime or sulphuric acid applied.

Comments: Similar relations between abundance and soil pH have been observed for several species in natural soils of different acidity (Hågvar & Abrahamsen 1984, Hågvar 1984b). In these soils, variations in soil pH were not brought about by extreme concentrations of the chemicals used in the experiments. The hypothesis is refuted.

Hypothesis 3

Observed relations in natural soils between pH and abundance of certain microarthropods are due to variations in factors correlated to soil pH, such as N-content, loss on ignition, humus type, or soil profile.

Comments: Similar faunal reactions to soil pH variations were observed in the liming and acidification experiments where the factors mentioned above were insignificantly affected by the treatments. The hypothesis is refuted. (Certail soil chemical parameters such as Ca and base saturation are, however, always linked to the pH level of the soil).

Hypothesis 4

The increased abundance of certain microarthropods in acidified samples is due to reduced predation pressure.

Comments: Microarthropods represent a suitable prey for several predators, especially for the larger predatory Gamasina mites (Mesostigmata). Increased abundance of Collembola in DDT-treated soil has been related to reduced numbers of Gamasina (e.g., Sheals 1956, Edwards et al. 1967). The abundance of these Gamasina was, however, largely unaffected by acidification. Furthermore, the increase of potential prey species often occurred below 3 cm depth, while the relevant predators live mainly in the upper 3 cm layer. The possibility exists, however, that other predators are important, for instance certain egg predators.

Hypothesis 5

The population changes were due to different food conditions at the various pH levels, especially the availability of fungal hyphae.

Comments: Fungal hyphae are found in the gut contents of many species and are generally considered to be an important food item for microarthropods. Relations between microarthropods and the fungal flora are, however, difficult to study. The following considerations disimply a simple connection between changes in the fungal flora and the microarthropod fauna:

- No significant changes in the fungal biomass occurred in one of the field experiments where characteristic faunal changes were observed (Bååth et al. 1979). Qualitative changes in the fungal flora and hyphae production per unit time were, however, not studied.
- The species which increase their abundance in acidified soil or litter show large variations in ecology and morphology (size, depth distribution, mouthparts, and gut contents). It is difficult to understand how certain changes in the fungal flora can affect these different species in the same way. Furthermore, various fungus-feeding species reacted differently to acidification (for example the common species *Isotomiella minor* was either unaffected or negatively affected by acidification, while another fungal-feeder, *Mesaphorura yosii*, often increased its abundance in acidified soil).
- Unpublished studies on the gut contents of *Mesaphorura yosii, Isotoma notabilis* and *Nothrus silvestris* from the colonisation experiment (Hågvar & Abrahamsen 1980) did not reveal drastic effects of the treatments. Besides measuring to what degree each gut was filled, and the percentage of empty guts, the gut contents were divided quantitatively into the following fractions: fungal spores, dark hyphae, light hyphae, brown particles (unidentified), amorphous material, and mineral particles.

Hypothesis 6

The fecundity (egg production) of certain species is directly related to soil pH (for instance via food quality).

Comments: Preliminary counts of ripe and developing eggs within *Tectocepheus velatus* from different treatments in the colonisation experiment and a field experiment are difficult to interpret, but do not clearly support the hypothesis.

Hypothesis 7

The population growth rate of certain species is correlated with the soil acidity.

Comments: In several experiments with acidification and liming it was found that microarthropod species, which were especially common at a certain treatment, also had a high percentage of juveniles in the relevant samples. These observations led to the hypothesis that there is a correlation between soil pH and reproductive success in several microarthropods. Also certain experiments and observations from the literature support this hypothesis. However, the observed high populations with a large fraction of juveniles can also be brought about by factors other than increased reproduction, for instance lowered mortality rates of eggs or juveniles.

An unpublished study was carried out to test Hypothesis 7. In three species, which in several experiments had shown increased abundance in acidified soil and reduced abundance in limed soil, the population growth at different pH levels was studied. The species were *Mesaphorura yosii* (Collembola), *Schwiebea cf. nova* (Astigmata), and *Nothrus silvestris* (Oribatei). When kept in pure culture at different pH levels, the population growth of each species could be related to the soil pH without being influenced by predators or interspecific competition. All cultures started with twenty animals, and extractions were made after 3, 6, and 12 months. This study showed that the three species did not repeat their characteristic reactions to soil pH when they were alone. In several samplings the trend was the opposite, i.e., the largest populations developed in limed samples. On this basis, the hypothesis can be refuted.

These considerations lead naturally to the next hypothesis.

Hypothesis 8

Competition between species is a major population-regulating factor, and at different soil pH levels, different species are favoured in the competition process.

Comments: The culture experiments with single species referred to above indicate that the »characteristic« reactions to soil pH changes occur only in the presence of other faunal elements. Competition studies may therefore lead to fruitful information. Even in the »colonizing experiment« where animals were allowed to colonize soil samples of different pH values, the establishment and development of the fauna in the samples occurred under continuous competition.

While competition may be a key word in explaining the observed results, the number of possible mechanisms is high. Several experimental approaches are probably needed.

At the present state of knowledge, some general considerations can be made. While it was stressed under Hypothesis 5 that the species increasing in acidified soil showed considerable differences in ecology (including feeding habits), these species do in fact have one important feature in common: they all belong to the most dominant microarthropod species in the raw humus soils used in the experiments. The natural pH of these soils was about 4.0, so the pH must be characterized as rather low even before the artificial acidification started. It is reasonable to assume that the factors initiating the increased abundance of these species during artificial acidification are the same factors which have induced their generally high dominance in naturally acid soils. By increasing soil acidity the relevant species may thus be increasingly favoured in the competition process. If competition is strong, the highest abundance under field conditions may be achieved under quite another pH value than that proved to be the optimal pH in pure culture.

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