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Effects of earthworms on plant growth: patterns and perspectives

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Summary

A total of 67 studies were located in which the response of plants to presence of earthworms was investigated. The number of studies increased strongly during the last decade. In most of the studies (79 %) shoot biomass of plants significanty increased in the presence of earthworms. However, knowledge on effects of earthworms on plant growth is very biased; most studies investigated crop plants, particularly cereals, and pastures; very little is known on plant species in more natural communities. Recently, interest in tropical plant species has increased considerably, however, the studies have considered almost exclusively agricultural plant species. Generally, experiments focused on the response of plant shoots but 45 % of the studies also considered roots. Most of the studies investigated European earthworms (Lumbricidae); very little is known on other earthworm species. Some early studies indicated that earthworms affect the composition of plant communities but only very recently has it been documented that earthworms affect plant competition. However, there is virtually no information on how earthworms affect plant performance in detail including fitness parameters such as flowering and seed production. It has been realized recently that earthworms not only modify plant growth and vegetation structure but also the susceptability of plants to herbivores. Herbivore performance might be stimulated but also reduced due to the presence of earthworms. Furthermore, earthworms function as subsidiary food resources to generalist predators when herbivore prey is scarce. The complex indirect interactions between earthworms and the aboveground system deserve further investigation in both natural and agricultural ecosystems. The imperative for future research is adopting an ecological rather than an agricultural perspective in studying earthworm-plant interrelationships and viewing earthworms as driving factors of the aboveground food web. It is suggested that studies on earthworm-plant interactions may contribute significantly to a more comprehensive understanding of terrestrial ecosystems and to the development of more environmentally friendly agricultural practices.

Key words: Lumbricidae, rhizosphere, animal-plant interactions, indirect effects, food-web

Introduction

Earthworms generally are assumed to be beneficial soil animals which is mainly based on the belief that they promote plant growth (Lee 1985; Edwards & Bohlen 1995). Scientists investigating effects of earthworms on plant growth have usually adopted an agricultural perspective by focusing on modifications in plant produc-

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tion, i. e. the yield of crop plants. Most studies have focused on arable species and little is known on the effect of earthworms on plant community strucure in more natural ecosystems. The studies reviewing earthworm-plant interactions (Brown et al. 1999; Brussaard 1999; Doube & Brown 1998; Baker 1998; Logsdon & Linden 1992; Edwards & Bater 1992) uniformly focused on arable systems. None of them worked out research needs for a better understanding of effects of earthworms on aboveground communities in natural habitats as mediated by modifications in plant growth.

Above- and belowground communities have largely been investigated independent of each other, however, recently interest is increasing to integrate below- and aboveground communities in a more holistic view of ecosystems (van der Putten et al. 2001; Scheu & Setälä 2002; Wardle 2002). Awareness is increasing that the belowground system cannot just be treated as a black box which functions to replace nutrients necessary for plant growth. In fact, the soil system is one of the most complex systems and it is obvious that the interactions between its components feed back to roots and therefore to plant growth. These feedbacks have been realized by earthworm ecologists since the very early studies by Darwin (1881) and except for plant parasitic nematodes earthworms have received most attention in studies on effects of belowground animals on plant performance. So far, however, these studies appear to be little recognized by ecologists working above the ground. This neglect may be caused either by the ignorance of ecologists working above the ground or by the fact that earthworm ecologists have failed in integrating the implications of their research field into general ecological thought.

This review intends to extract patterns in studies on earthworm-plant interactions. Based on these patterns research deficits and priorities for future work are delineated. The study aims at fostering the view that belowground communities are essential parts of ecosystems and the interactions therein need consideration for a more comprehensive understanding of their functioning. Earthworm ecologists may contribute substantially to achieve this goal.

Patterns

I compiled studies on earthworm-plant interactions by searching the Web of Science database for the years 1949 to 2002. In addition, references of my own database were added which also includes conference proceedings and book chapters. Only studies presenting data on effects of earthworms on plant growth, i.e. plant height or biomass production were considered. A total of 67 studies reporting 83 cases on how earthworms affected plant growth were included (Appendix). Results of the extensive study on the effects of earthworms on tropical crop species given in Brown et al. (1999) were not included because of incomplete data presentation. To work out temporal trends the studies were divided into three periods, before 1981, 1982 to 1991 and 1992 to 2001. Of the 67 studies 16 were from the first period, 12 from second and 39 from 1992 until present indicating a strong increase in the interest in earthworm-plant interactions during the last decade. Since the great majority of the studies focused on agricultural plant species (see below) this increase reflects the growing interest in more environmentally friendly agricultural practices such as integrated or organic farming systems.

Irrespective of the period considered the great majority of studies only investigated a single plant species (Fig. 1). Prior to 1992 there were no studies on two species combinations and very few considering more than two species. The number of studies investigating plant mixtures (exclusively pastures) was low and remained very constant. Overall, the number of plant species considered in studies on earthworm effects on plant growth was very constant. Research remains very much biased towards very simple systems containing a single plant species. This conclusion is supported by the fact that the great majority of studies were done in pots in the laboratory (71 %), only 9 % (before 1981), 33 % (1982–1991) and 11 % (1992–2002) were done in field plots. A distinct pattern was the increase in the fraction of studies investigating tropical plant species from 6 % before 1981 to 9 % in the period 1982–1991 and to 15 % in 1992–2002. Considering the extensive

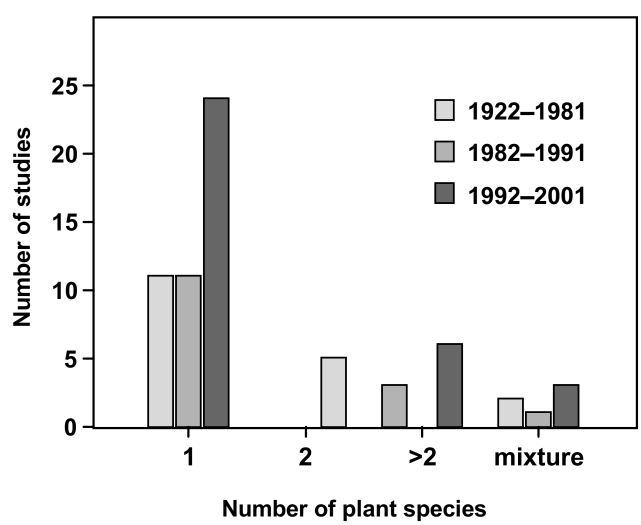

Fig. 1. Number of plant species considered in studies on effects of earthworms on plant growth in the periods 1922–1981, 1982–1991 and 1992–2001

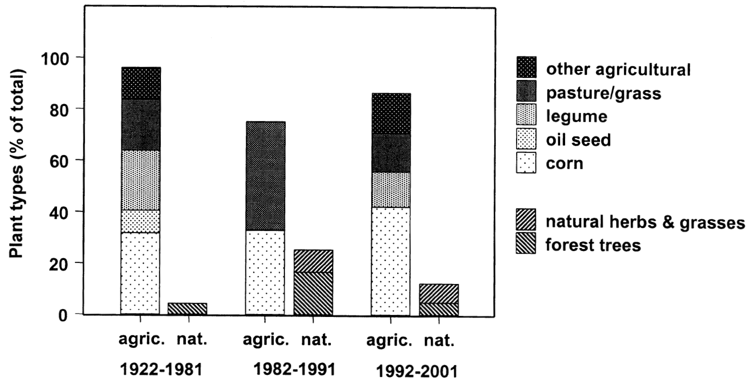

Fig. 2. Plant types considered in studies on effects of earthworms on plant growth in the periods 1922–1981, 1982–1991 and 1992–2001; plants from agricultural (agric.) and natural (nat.) communities are distinguished

study of Brown et al. (1999) which was not included in the dataset the number of studies investigating tropical plant species even exceeds that of studies on non-tropical species in 1992–2001.

To evaluate if plants respond differently to the presence of earthworms the following plant types were distinguished: corn, oil seed plants, legumes, pasture grasses, other agricultural plants including trees, forest trees and natural herbs/grasses. The latter two represent plant species from more natural communities while the first five represent agricultural species. In general, agricultural plants dominated strongly with 96 %, 75 % and 88 % of the species in the periods before 1981, 1982–1991 and 1992–2001, respectively (Fig. 2). Respective numbers for forest trees were 4 %, 17 % and 5 %. There was no study on natural herbs and grasses before 1981 in the database; only a single study (8 %) investigated natural herbs in 1982–1991 and this changed only a little in 1992–2001 (4 studies, 7 %). Obviously, effects of earthworms on plant growth in more natural plant communities have been largely ignored. In agricultural plants cereals and grasses (pasture) dominated; considerably less is known of the response of legumes and oil seed plants. Studies in the tropics are also biased towards agricultural species with a single experiment considering fruit trees (Pashanasi et al. 1992).

In most of the studies (79 %) shoot biomass was increased in the presence of earthworms, but in 9 % of the experiments it declined and in 12 % no significant effect was found. The response of root biomass is documented in 45 % of the studies and was less consistent than that of shoots with an increase in 50 % but a decrease in 38 % of the cases. Non-significant or negative effects of earthworms often were reported for legumes, indicating that different functional groups of plants respond differently. The shoot-root ratio was only studied in 24 % of the cases. However, in contrast to root biomass it uniformly increased in the presence of earthworms, except of a single study which reported a decline (Atiyeh et al. 2000).

In the great majority of cases effects of earthworms on plant growth were evaluated by sampling plants only once (76 %). Very few studies investigated the response of plants in more detail; only 8 % of the studies sampled more than three times. A detailed analysis on how earthworms modify plant development is lacking. Similar to plant species knowledge on the effect of different earthworm species on plant growth is very biased towards widespread inhabitants of agricultural systems. The majority of studies investigated European species (82 % of total) most often endogeic forms (50 % of total), in particular *Aporrectodea caliginosa* (Fig. 3). Anecic (20 % of total) and particularly epigeic species (9 %) received little attention. Generally, the proportion of earthworm groups studied changed little during the the last century with the exception of an increase in study of non-European species starting with the period 1982–1991.

There were strong changes in the way of publication of studies on earthworm-plant interactions. Prior to 1982 most studies were published in agricultural journals (38 %; Fig. 4) whereas today soil biology journals predominate (77 % of all the studies in 1992–2002). Remarkably, only few studies (6–13 %) were published in general ecological journals which certainly contributes to the low awareness of the topic among ecologists working above the ground.

The recent review article of Crooks (2002) on invading species as ecosystem engineers examplifies the ignorance of ecologists on the role of earthworms for community functioning and ecosystem properties. Due to the activities of man European earthworm species but also tropical species are spread all over the world (Reynolds 1998; Baker 1999; Fragoso et al. 1999). The invasion of earthworms has been shown to transform soil systems from moder to mull type humus due to physical action, i.e. by engineering (Langmaid 1964; Alban & Berry 1994; Scheu & Parkinson 1994a; McLean & Parkinson 1997; Burtelow et al. 1998). Knowledge on the impacts of this transformation is still limited, however, strong effects on soil microorganisms, soil microarthropods, nutrient dynamics and

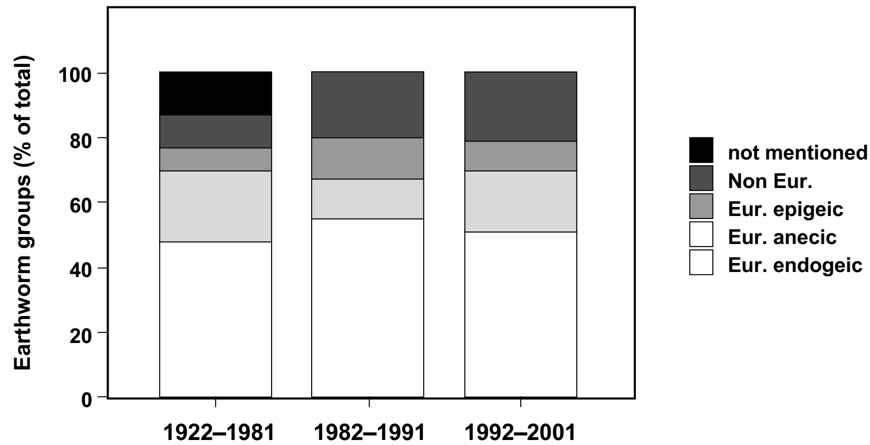

Fig. 3. Earthworm species used in studies on effects of earthworms on plant growth; earthworms of different geographical region/origin and ecological group were distinguished

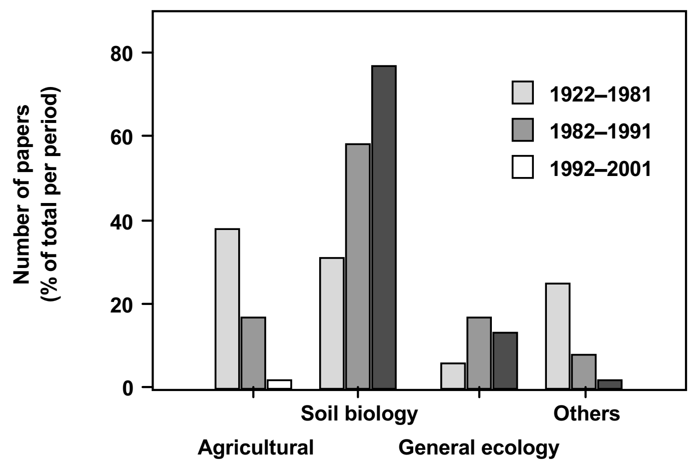

Fig. 4. Journals in which studies on effects of earthworms on plant growth were published; among others agricultural journals include Soil Science, New Zealand Journal of Agriculture; soil biology journals include Soil Biology and Biochemistry, Pedobiologia, Applied Soil Ecology, Biology and Fertility of Soils; general ecology journals include Ecology, Oikos, Oecologia; others include Plant and Soil and book chapters

plant growth have been documented (Scheu & Parkinson 1994b; Burtelow et al. 1998; McLean & Parkinson 1998a,b, 2000; Migge 2001). Despite the fact that the global dispersion of earthworms results in one of the most dramatic and large-scale transformations of ecosystems and these transformations are due to engineering this is hardly touched upon in the review of Crooks (2002).

Perspectives

Earthworms have been documented to be major driving forces for belowground processes. Due to their large body size, high consumption rates and burrowing activity they are keystone organisms forming the habitat of soil biota (Bal 1982; Lee 1983; Anderson 1988; Lavelle et al. 1997). Also, it has widely been appreciated that earthworms affect decomposition processes and nutrient dynamics in soil (Lee 1985; Blair et al. 1995; Edwards & Bohlen 1995; Parmelee et al. 1998). However, as outlined above, the implications of these effects for the aboveground system are strongly biased towards agricultural systems and focused on a single parameter, the yield of crop plants. It appears that earthworms have been treated largely as agents for improving agricultural production rather than as components of natural ecosystems. As indicated by the change in the journals in which results of earthworm-plant interactions are published, earthworm ecologists no longer see their subject as part of the agricultural sciences. However, as stressed previously, the penetration of results from studies on earthworm ecology and soil ecology in general into general ecological thought is regrettably poor (Lee 1992; Eijsackers 2001).

The lack of integration of studies on effects of earthworms on plant performance and the whole aboveground system opens a large scope for future research. The imperative for future research is adopting an ecological rather than an agricultural perspective in studying earthworm-plant interrelationships and viewing

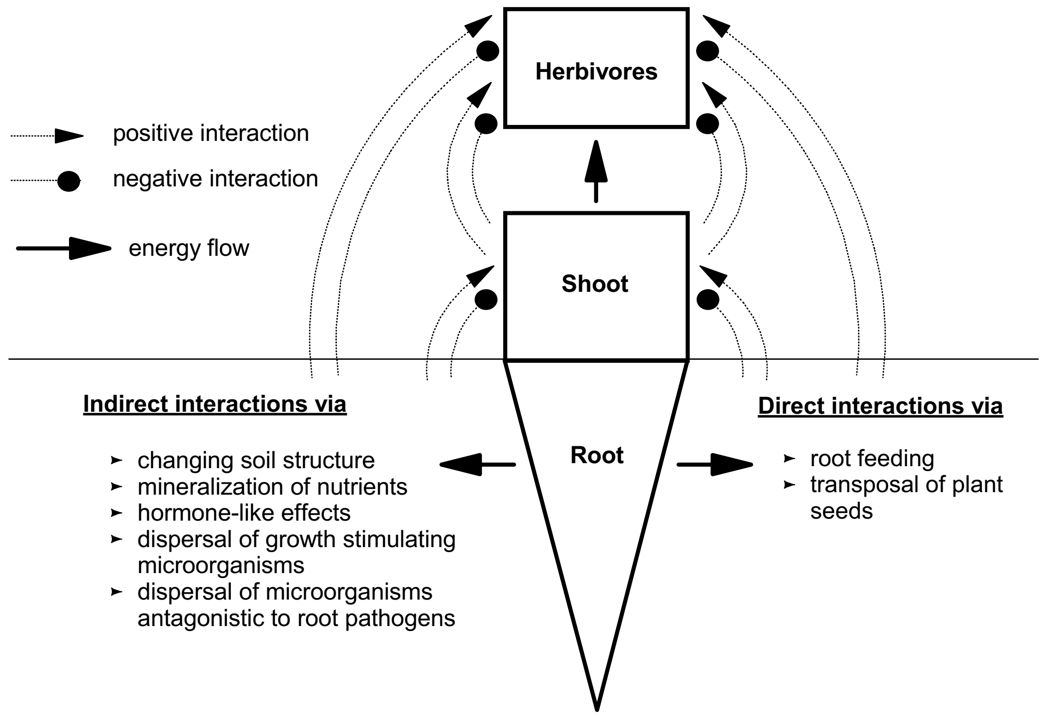

Fig. 5. Mechanisms by which earthworms affect plant growth and the herbivore community above the ground (modified from Scheu & Setälä 2002)

earthworms as driving factors of the aboveground food web. Earthworms not only modify nutrient availability to plants but may alter the whole rhizosphere environment. The mechanisms by which earthworms affect plant growth include direct effects such as root feeding and transposal of plant seeds. However, plant growth is modified mainly indirectly by changing soil structure, mineralization processes, hormone-like effects, dispersal of plant growth stimulating microorganisms and dispersal of microorganisms antagonistic to root pathogens (Fig. 5). As stressed by Scheu (2001) and Scheu and Setälä (2002), belowground interactions may not only affect plant growth and vegetation structure but further propagate into the herbivore and even predator/parasitoid community.

Mechanisms of earthworm-mediated changes in plant growth

As outlined above earthworms modify plant growth by a multitude of mechanisms. A detailed discussion of these mechanisms is beyond the scope of this article, however, I would like to stress that a better understanding of these mechanisms is essential for a more complete appreciation of the role of earthworms for plant growth and vegetation development. However, studies so far have focused almost entirely on earthworm-mediated changes in the nutrient availability to plants, i.e. on one of the indirect ways in which earthworms modify plant growth. The importance of other indirect effects and also that of direct effects has been little explored. Of course, it is often very difficult to ascribe earthworm-mediated changes in plant growth to a single mechanism since earthworms change a number of factors which may affect plant growth simultaneously. However, efforts to single out specific mechanisms have been limited so far. For example, to exclude nutrient effects experiments may be set up in which the nutrient demand of plants is saturated by fertilization. No such experiments have been performed so far. Also, genetically modified plants, e.g. those deficient in ability to respond to certain nutrients, may help in exploring earthworm-plant interrelationships.

Plant performance and vegetation structure

Even more important than a better understanding of the mechanisms of how earthworms affect plant growth is a widening of the plant perspective. The focus has to shift from the yield of agricultural plants to the performance of plants in natural communities. As outlined above plants of different functional groups differ in their response to the presence of earthworms. Surprisingly, so far the consequences of this differential response for the interaction between plant species and therefore for vegetation development have hardly been investigated. Also, direct effects of earthworms on plants via translocation of seeds has been little explored. Earthworms, particularly anecic species, are known to ingest plant seeds which results in seed removal from the soil surface but also in translocation of buried seeds to the soil surface thereby affecting germination of seeds by exposure to a different environment (McRill & Sagar 1973; Grant 1983; van der Reest & Rogaar 1988; Shumway & Koide 1994; Thompson et al. 1994; Willems & Huijsmans 1994). In addition, germination of seeds is affected by the earthworms themselves as the gut passage and factors in earthworm faeces may break seed dormancy (Kollmannsperger 1952; Ayanlaja et al. 2001). Seed translocation and the modification of germination may play an important role in vegetation development as shown in model ecosystems (Thompson et al. 1993); evaluating the importance of these processes in natural plant communities is a promising topic for future research.

The plant root system is being recognized as a foraging system searching for, occupying and defending resources in soil (Fitter 1994; Hutchings et al. 2000). Plant species differ strongly in the way they search for resources and the distribution of resources in soil is an important driving factor for plant growth and plant competition (Hodge et al. 1999, 2000). Earthworms govern the distribution of organic matter in soil and therefore likely affect root foraging. In fact, as indicated by the recent study of Wurst et al. (2003), grasses benefit more from aggregated organic matter distribution in soil than legumes and tap root species such as *Plantago*, and the response of the plants to organic patches is modified by earthworms. The impact of earthworms on resource distribution in soil may explain in part the differential response of plant species to the presence of earthworms (see below).

It has been realized in early studies that the presence of earthworms may alter the structure of plant communities. Hopp and Slater (1948) documented that the dominance ratio between grasses and legumes shifts towards the latter in experimental grassland systems with earthworms. Hoogerkamp et al. (1983) reported that compared to herbs grasses benefit more from earthworm inoculations into polder soils. In contrast, in the experimenal plant community of Thompson et al. (1993) clover was more responsive to earthworm presence than grasses and herbs. Schmidt and Curry (1999) reported that wheat benefits more from earthworm presence than clover. Consistent with these findings the growth of *Poa annua* was increased much more by earthworms than that of *Trifolium repens* in the study of Scheu et al. (1999). Similarly, in a recent experiment (K. Kreuzer & S. Scheu, unpubl. data) *Lolium perenne* benefited more from the presence of earthworms than *T. repens* (Fig. 6). Generally, in this experiment *T. repens* dominated but if earthworms and collembolans were present *L. perenne* successfully competed for resources with *T. repens*.

Studies on effects of earthworms on plant growth have so far focused on gross yield parameters such as biomass of plant shoots or grains (in cereals; see above). As indicated by the study of Kreuzer and Scheu (unpubl. data; Fig. 6) the strengthening of the competition of *L. perenne* was caused at least in part by an increase in the number of shoots. Obviously, earthworms not only modify plant biomass production but also the growth form of plants. This certainly also applies to their belowground parts. For roots there is also hardly any information except on root biomass; I am not aware of any study investigating earthworm effects on the structure of plant root systems. For understanding the mechanisms by which earthworms affect plant competition modifications of the rooting system needs to be investigated. Furthermore, earthworms likely affect plant phenology, i.e. the duration of vegetative and generative phases, plant reproductive parameters such as numbers of flowers and seeds, and even pollination processes (K. Poveda, pers. comm.). In fact, it has been documented that e.g. *P. annua* flowered two weeks earlier in the presence of earthworms and earthworms also increased the number of inflorescences (Scheu et al. 1999).

Another ignored topic in experiments on how earthworms affect plant growth is the physiological response of plants. It has been documented frequently that the presence of earthworms results in increased nutrient concentrations in plant tissue (Alphei et al. 1996; Callaham & Hendrix 1998; Schmidt & Curry 1999; Bonkowski et al. 2001). As the major limiting element for plant growth the availability of nitrogen

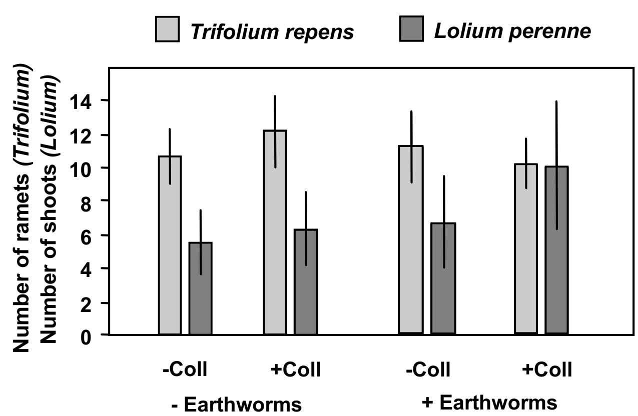

Fig. 6. Effects of earthworms and collembolans on the competition between *Trifolium repens* and *Lolium perenne* as measured by the number of ramets and the number of shoots, respectively (means with 1 SD; K. Kreuzer & S. Scheu, unpubl. data)

drives plant physiology. Earthworms therefore likely affect the concentrations of primary and secondary metabolites in plants and this may have important consequences for the susceptability of plants to pathogens, parasites and herbivores. In fact, early observations by Kollmannsperger (1952) indicate that earthworm faeces increase the resistance of cress seedlings to fungal pathogens which he ascribed to the uptake of antibiotics produced in the rhizosphere. These interesting findings have not been followed up. However, it has been documented that earthworms may reduce the severity of soil borne plant deseases by changing the soil microbial community (Stephens et al. 1993, 1994a,b,c; Stephens & Davoren 1997; Clapperton et al. 2001). Earlier studies documented that leaf burial by anecic earthworms contributes to the reduction of pathogenic fungi in orchards (Raw 1962; Niklas & Kennel 1981). The implications of these findings for natural plant communities remain to be investigated.

Herbivore performance

Herbivore performance is known to strongly depend on plant tissue nitrogen content, and as documented above earthworm-mediated changes in plant growth often are associated with an increase in plant tissue nitrogen content. Therefore, effects of earthworms on plant growth likely propagate into the herbivore system. In fact, it has been documented that earthworms stimulate the reproduction of aphids on grasses and legumes (Scheu et al. 1999). However, the effects of earthworms on herbivores above the ground likely vary with soil and depend on plant species. Bonkowski et al. (2001) did not find significant changes in aphid reproduction on wheat and, depending on the distribution of organic resources in soil and on plant species, Wurst et al. (2003) documented that aphid reproduction may not be affected, or reduced, in the presence of earthworms. The reduction of aphid reproduction which only occurred on *Plantago* likely was caused by changes in plant defense compounds indicating that it is not only belowground herbivores but also decomposers that affect plant defense against herbivores (cf. van Dam et al. 2002). If decomposer organisms in fact modify the production of plant defense compounds this has strong implications for agricultural practices and opens a fascinating topic for future research.

As stressed in the introduction, recently the interest in links between the below- and aboveground system has increased strongly (van der Putten et al. 2001, Scheu & Setälä 2002, Wardle 2002). Various studies have documented that belowground herbivores may be important driving factors for the aboveground community (Masters et al. 1993; van der Putten et al. 1993; Ganade & Brown 1997; van der Putten & Peters 1997; Mortimer et al. 1999). It is surprising that despite the very obvious link between decomposers and plant growth their effect on the herbivore community went unrecognized until recently. Since decomposers like earthworms are almost ubiquitous and affect plant growth in a multitude of ways (Fig. 5) their effect on the herbivore system may well be more important than that of belowground herbivores as stressed previously (Scheu 2001).

This also opens a fascinating research field for earthworm ecologists. One of the most important herbivores belowground are nematodes and nematodes are known to be digested by earthworms thereby functioning as predators (Hyvönen et al. 1994). In this way earthworms may function as plant mutualists reducing the severity of herbivore attack thereby also modifying the susceptability of plants to aboveground herbivores. It is increasingly recognized that complex trophic interactions are more important than previously assumed (Olff et al. 1999; Tscharntke & Hawkins 2002). So far decomposers such as earthworms have been widely neglected in the interplay between trophic levels.

There is another mechanism by which decomposers may affect herbivore performance above the ground which has been termed the microbi-detritivore – generalist predator – herbivore pathway (Scheu 2001). Decomposer invertebrates are known to be important food resources for generalist predators above the ground. Earthworms form a substantial part of the diet of aboveground invertebrate predators, such as carabid beetles (Lukasiewicz 1996; Guillemain et al. 1997), but also of vertebrate predators particularly birds but also boars, hedgehogs, badgers and foxes (Bengtson et al. 1976; Macdonald 1983; Doncaster 1994; Micol et al. 1994; Roper 1994; Cherenkov et al. 1995; Ferrari & Weber 1995; Baubet et al. 1997). Earthworms therefore contribute to maintaining populations of generalist predators above the ground and by switching to aboveground herbivore prey species generalist predators may help in controlling pest species of crop plants. In fact, Symondson et al. (2000) documented that earthworm prey may help sustain the populations of the slug feeding carabid beetle *Pterostichus melanarius* in arable land. Since generalist predators are opportunistic feeders they may switch from decomposer prey species to herbivores when the density of decomposer species declines and that of herbivores increases. This likely occurs with the onset of the growth period (Settle et al. 1996). Plants strongly increase the loss of water from the soil to the atmosphere and therefore with increasing vegetation development the soil gets dryer. Decomposer animals including earthworms are very sensitive to desiccation and retreat to deeper soil layers when the soil is becoming dryer. On the other hand, the development of plants is followed by that of herbivores and their contribution to the diet of generalist predators then likely increases. It is challenging to test this hypothesis in future and to evaluate to what extent the decomposer community contributes to the dynamics between predators and herbivores above the ground. A closer investigation of these relationships may help in developing more environmentally friendly agricultural practices.

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Appendix. Authors and date of publication of studies included in the survey on effects of earthworms on plant growth*

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* A list with full references can be obtained from the author