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Research on subsoil biopores and their functions in organically managed soils: A review

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Abstract

The living soil is the basis for crop production in organic agriculture. Biopores are voids in the soil which were formed by the activity of soil life. The first scientific studies on biopores were published in the 1870s–90s by Victor Hensen who stated that earthworms were opening channels to the subsoil and coating them with humus, thus creating a beneficial environment for root growth. His work was originally widely recognized, but then research on biopores was neglected for many decades and was only revitalized with the rise of ecological concerns in the 1960s. In recent times, biopores have attracted the attention of agronomists with a focus on organic agriculture. New visualization techniques, such as X-ray micro computed tomography, *in-situ* endoscopy and nuclear magnetic resonance imaging have been applied. Biopores contribute to air transport through the soil, increase water infiltration, reduce water runoff and soil erosion, serve as preferential pathways for root elongation and can facilitate the acquisition of water and nutrients from the subsoil. The relevance of biopores for nutrient acquisition can be pronounced particularly in organic production systems, where crops are more dependent on nutrient acquisition from the solid soil phase than under conditions of conventional agriculture. Organic land-use strategies should aim to increase number, stability and quality of biopores. The biopore density can be increased by the share of dicotyledons in the crop rotation and by cultivating perennial crops with taproot systems. Moreover, density and—in particular—the quality of biopores, e.g., the nutrient contents of pore walls, can be influenced by anecic earthworms which can be promoted by adapted tillage practices.

Key words: biopores, soil fertility, nutrient acquisition, root growth, water infiltration, gas exchange

Introduction

Biopores are voids in the soil which were formed by biological activity. In general, biopores can have diameters from <30 μm (these are for instance the pores created by enchytraeids or root hairs) up to >5 mm[1]. Typically the term biopores refers to tubular shaped, continuous pores formed by plant roots and burrowing soil animals such as earthworms (Fig. 1). In most agricultural soils, the largest biopores are the burrows of anecic earthworms. For instance, the channels created by *Lumbricus terrestris* L. have an average diameter of 9.4 mm[2]. Larger voids, such as the channels created by moles, have been attributed to biopores as well[3], but they do not cover large areas in agricultural soils and are therefore not included in this review. Despite studies on biopores often focusing on earthworm burrows and other coarse pores, over 80% of the biopores per unit area can have a diameter of less than 1 mm[4]. Biopores are present throughout the soil profile, from the surface to several meters in depth. In arable soils, tillage frequently destroys biopore systems in the plough horizon, but not in the subsoil. Biopores >30 μm in diameter provide channels for new root growth and water and air conduction[1]. In the subsoil—which is generally assumed to be relatively compact and poor in nutrients—biopores are supposed to have a special relevance for root growth[5] (Fig. 2) and serve as hot spots for nutrient acquisition of crop roots[6]. In organic farming systems, facilitation of root growth and nutrient uptake can have particular relevance since the availability of nutrients is generally limited[7]. For instance, synthetic mineral fertilizers are not permitted in organic agriculture in the European Union (Council Regulation (EC) No. 834/2007). Instead, organic farming strategies aim to close nutrient cycles as much as possible[8] and to mobilize nutrients from the solid phase. Thus, extensive and active root systems can contribute to nutrient acquisition.

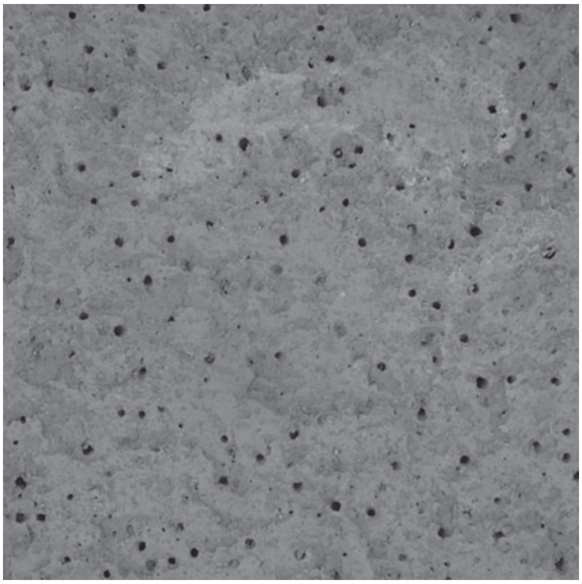

Figure 1. Biopores in 45 cm soil depth (top view). The picture covers approximately 50 × 50 cm.

Starting from the 19th century, studies on biopores were inspired by advances in the field of ecological sciences. In turn, research on biopores contributed to a deeper understanding of soil ecological processes, providing a background of knowledge for organic management of soils. Against this background, this article reviews research on biopores from its beginnings to date, summarizes the current state of knowledge about the functions of biopores in agricultural soils and outlines possible consequences for organic management.

Biopores Through the Ages: Ecology and Biopore Research

Biopores as objects of research do not appear in the literature until the second half of the 19th century. One apparent reason for the long inobservance of biopores is that they were hardly recognized before soil was studied extensively, i.e., before trenches or pits were arranged and biopores were dissected. In fact, soil was seldom studied below a depth of a few centimeters until soil science as a natural science was established by V. V. Dokuchaev in the 1870s and 80s. Prior to this, however, it was a crop scientist named Hugo Thiel who first studied root growth in a clover field as part of his dissertation research[9]. In 1865, Thiel observed that roots were proliferating through previously existing channels especially in the subsoil. Thiel[9] already noted that these channels (‘*canales*’) were made by roots or soil animals. He counted 5–20 channels on 900 cm^2 in 2 m soil depth. However, to commence in-depth research on biopores it was necessary to research more about their functions. In other words, it was necessary to study how soil organisms (explicitly roots and earthworms) interact with each other and with their abiotic environment (mineral and organic particles, air and water). Thus, research on biopores required, by definition, *ecological thinking*. The first researcher who published studies on the properties of biopores was, using current science nomenclature, an ecologist—Victor Hensen, a marine biologist who is known as ‘the father of quantitative plankton ecology’[10]. In 1877, Hensen[11] reported on the burrowing activity of earthworms in his garden. He concluded that earthworms were opening channels to the subsoil and that they were coating them with humus, thus creating a beneficial environment for root growth. Moreover, Hensen[11] made the first remarks on the dynamics of the biopore properties over time, reporting that the walls of fresh pores were covered with dark humps made up of earthworm excreta, whereas the walls of older pores, no longer colonized by worms, were uniformly covered with dark soil originating from earthworms. He also mentioned pores completely filled with dark soil that he assumed to ‘diffuse’ into the surrounding soil and to weather over time, until only unfertile soil remains. Hensen[12] clearly pointed to the relevance of earthworm channels for roots as a fertile environment with a low penetration resistance, stating, ‘More beneficial conditions for the growth of plant roots may hardly be found …’. In a following publication, Hensen[13] provided detailed drawings of roots growing through biopores. Although he did not use the term ‘biopore’ and was

Figure 2. Biopore (longitudinal section). Soil depth approximately 50–80 cm.

focused on pores that were clearly earthworm channels, he also reported on fresh roots following the void created by a decomposing old root. Moreover, one of his drawings shows a pore 'not yet' coated with excrement, but containing a plant root. This pore may have been a pore originating from roots or a pore not colonized by an earthworm for a long time.

Hensen's first publication was cited by Charles Darwin[14] in his influential book *The Formation of Vegetable Mould Through the Action of Worms*, published in 1881. Interestingly, Darwin noted that some of his own observations 'have been rendered almost superfluous' by the 'admirable' paper by Hensen[11]. Hensen's work was widely recognized, especially by agricultural scientists and practical farmers, and encouraged some of them to undertake their own studies on earthworm activity and biopores and to discuss the role of biopores for crop production. For instance, Albert Schultz-Lupitz[15] postulated the guiding principle of crop production that crop farmers can stimulate root development by supporting the prosperity of subterranean animals such as earthworms. Furthermore, Ewald Wollny was inspired by Hensen's publications and conference contributions. Wollny had a special interest in soil physics and—different from the more agrochemical-oriented mainstream of his time—highlighted the importance of soil structure for the performance of crops. In column experiments, Wollny[16] documented that incubation with earthworms increased the permeability of soil for air and water.

Moreover, the role of biopores as pathways for preferential water flow was already described by the end of the 19th century. In 1881, Lawes et al.[17] noted that after heavy rainfalls, some water drained off through open 'channels' before the soil became saturated. However, this finding was not quantified and did not result in further investigations for many years.

After the first 'wave' of biopore research at the end of the 19th century, studies on biopores became rare during the following decades. In the early 20th century, many technical advances in agriculture were made, including the fabrication of mineral nitrogen (N) fertilizer based on the Haber–Bosch process. During this era many agronomists emphasized the question of how crops can be supplied with optimum amounts of nutrients rather than studying natural resources and their functions. Moreover, since the early 1940s major advances were made in development and application of chemical pesticides, which was also described as the beginning of the 'organic pesticide era'[18]. In contrast to the documentation of obvious yield increases resulting from mineral fertilization and pesticide application, it was more difficult to quantify the effect of earthworm activity and biopores on crop growth, holding all other factors influencing plant growth constant; thus only a few reliable studies were published during that era[19].

The interest in biopores was revitalized in the 1960s. By that time, ecologists expressed major concerns about the application of chemicals in agro-ecosystems. Rachel Carson's book *Silent Spring*[20] (1962), systematically criticizing the widespread use of pesticides from an ecological point of view, is often regarded as the beginning of the modern environmental movements[21], followed by an increased ecological awareness in the 1960s and 1970s. Certainly, it must be seen in this historical context that research on natural soil functions and their relevance for crop production was boosted in that time. Among other aspects of soil fertility, interest in biopores increased for soil scientists, agronomists and soil ecologists.

By this time, ecology was increasingly recognized as a distinct independent academic discipline. This nascent field of study was advanced through the seminal textbook *Fundamentals of Ecology* by Eugene P. Odum in 1953[22], which also helped to establish the concept of ecosystems. The ecosystem concept, which postulates the presence of open sub-systems within the biosphere that are defined by the interactions between organisms and their abiotic environment, had been originally developed by Tansley in 1935[23]. The application of this concept to soil allowed the understanding of soil as a complex network of activity by soil animals, microorganisms and roots, and their interaction with water, gasses, mineral and organic particles. Biopores evidently are implied as specific areas of interest as a living space for soil organisms within this network.

With this new system-oriented view, pores created by soil animals or plant roots were now understood as a functional unit. Newly developed methods, such as the microscopic investigation of soil peels[24,25], also allowed quantification of pores on a much smaller scale. However, while large earthworm burrows can be identified with comparative ease by their characteristic coatings and typical dark-colored surface, the origin of pores with smaller diameters often remained unclear. In 1964, Slager[26] overcame this methodological problem by combining investigation of pores from different origins and being the first to use the word 'biopore' as a superordinate concept for pores generated by animals or roots.

Also in the 1960s and 1970s, much progress was made in characterizing the chemical properties of the surroundings of biopores. For instance, Graff[27] studied the downward transport of nutrients by earthworms and quantified the enrichment of N, phosphorus (P), potassium (K) and calcium (Ca) in the pore wall. Furthermore, earthworm channels were shown to have beneficial effects on biomass and nutrient contents of crops in pot experiments[28] and field studies[29]. Graff[30], referring to the history of agriculture, appreciated the pioneering role of Victor Hensen for research on earthworms and biopores. As researchers became more interested in the 2 mm zone around earthworm burrows as a place of increased concentrations of nutrients and soil organic matter, it was denoted as the 'drilosphere' by Bouché[31]. The role of biopores in soil hydrology also received increasing attention, as well as initial suggestions for supporting the formation of biopores through agronomic measures. For instance, Ehlers[32] highlighted the relevance of biopores for water infiltration and demonstrated the possibility of increasing the number of biopores per unit area by a reduction of tillage intensity.

Advances in computer applications made during the 1980s allowed the use of computer models to predict the influence of biopores on root and shoot growth of crops[33]. A model developed by Jakobsen and Dexter[34] predicted that biopores made significant contributions to root penetration, but resulted in reduced water availability during the grain-filling period due to increased early water use[35]. In the 1990s the newly developed concept of ecosystem engineers again drew attention to biopores. Ecosystem engineers are organisms that 'modulate the availability of resources to other organisms by causing physical state changes in biotic or abiotic materials'[36]. In this context, researchers focused on earthworms and roots as ecosystem engineers that both create biopores with subsequent new living spaces for soil organisms[37]. Furthermore microbiological methods such as enzyme assays became widespread during the 1990s, allowing more detailed understanding of the biochemistry of biopore walls[38].

In recent times, biopores have attracted the attention of agronomists who focus on their relevance for crop performance. For instance, biopores and their implications for root growth and water percolation were studied in hard-setting clay soils which severely restrict penetration by crop roots[39,40]. In addition, researchers oriented toward organic or sustainable agriculture focus on the biopores' functions, such as improving the water supply to crops or providing hot spots for nutrient acquisition contributing to plant nutrition[41]. When the topsoil is dry or poor in nutrients, organic farming or low input systems can particularly benefit from biopores[6]. This is an example of a management strategy in organic agriculture that incorporates recent ecological knowledge[42]. Developing strategies for creating, maintaining and using biopores is inherent to organic agricultural production, as well as in conventional systems that utilize conservation management practices such as no-tillage and cover cropping. Nevertheless, many questions on biopores and their effects on soil fertility and root growth remain unanswered. Future fields of research include the quantification of root–soil contact in biopores, nutrient uptake from the drilosphere and the temporal dynamics of biopore networks as a consequence of root growth, earthworm activity and abiotic factors. Presumably, future studies on biopores will increasingly rely on new visualization techniques, such as X-ray micro computed tomography which can create three-dimensional X-ray images[43]. For visualization of root growth in biopores new approaches have recently been described and will probably contribute to our understanding of nutrient acquisition from biopores. *In-situ* endoscopy[44,45] (Fig. 3) allows direct observation of roots growing in biopores, and nuclear magnetic resonance imaging allows the measurement of both root dynamics and earthworm activity in undisturbed soil cores[46]. Recently, the effect of biopores was integrated into a crop model solution, demonstrating the importance of biopores for root growth, water and nutrient uptake of spring wheat on soils with pronounced subsoil clay accumulation[47]. However, more research is needed to check the applicability of this result for other crops and soil types.

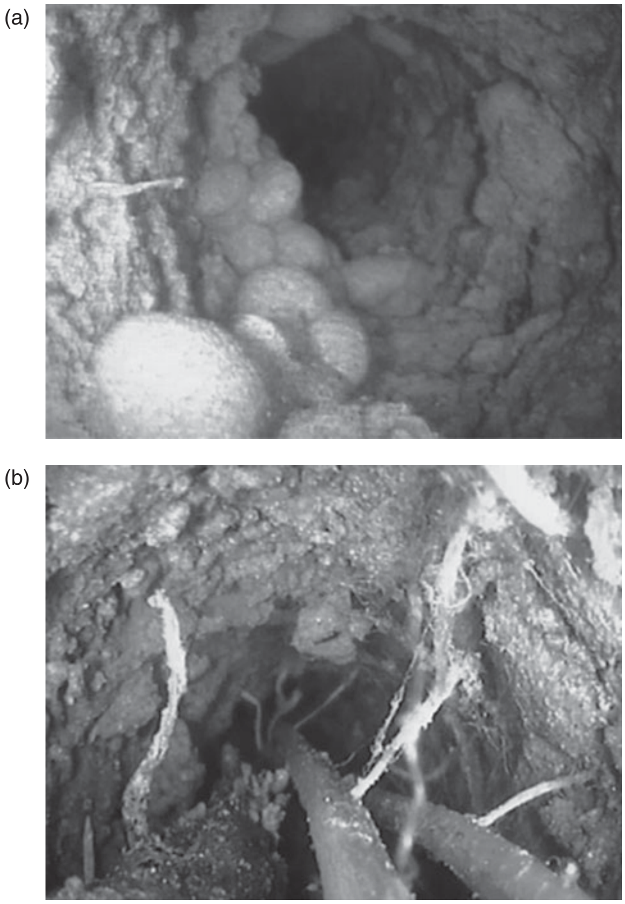

Figure 3. Endoscopic views into biopores: (a) biopore coated with earthworm feces; (b) biopore containing two vertical roots of *Brassica napus* and an older, decomposing root from a previous crop.

Functions of Biopores in Agricultural Soils: Current State of Research

Gas exchange, water infiltration and water percolation

Biopores contribute to the transport of air[48] as well as water and solutes[49] through the soil. The transport of oxygen from the soil surface to deeper soil layers through the soil matrix primarily occurs by gaseous diffusion[50]. Oxygen concentration of soil air generally decreases with increasing depth as a consequence of length and tortuosity of the diffusion pathway[50,51]. In contrast, vertical continuous biopores provide straight paths of diffusion in the soil. Furthermore, there is evidence for convection through large continuous biopores[52]. Hence, the oxygen concentration inside these biopores remains relatively stable throughout the soil profile[53].

Large-sized biopores drain rapidly and become air-filled after rainfall events[52]. Under wet conditions the air permeability of a clay soil was found to be greater vertically than in the horizontal direction, which can be explained by the presence of vertically oriented biopores[54]. As a result, elevated oxygen concentrations in biopores may have an effect on microbial activity and nutrient uptake by roots limited by a lack of oxygen in a dense subsoil[55,56].

Biopores with diameters larger than 0.3–0.5 mm support non-equilibrium water flow[57]. After rainfall events, water is transported downwards predominantly through large continuous pores. A single pore of 3 mm diameter can contribute more to water infiltration rate than the infiltration through the soil matrix in a 30 cm diameter area[58]. Macropore flow can be substantially enhanced after cultivation of alfalfa (*Medicago sativa* L.), a taprooted crop which can increase the number of continuous soil pores[59]. Positive correlations were found between the number of pores having diameters $\geqslant 2.0$ mm per area unit and both hydraulic conductivity and air-filled porosity[60]. In a sandy loam from an organic dairy farm the number of earthworm burrows and consequently hydraulic conductivity was found to be higher than in a similar soil under conventional management[61]. Increased water infiltration rates can have beneficial effects on soil fertility on arable land because they (1) reduce the risk of water ponding on flat terrain and (2) reduce water runoff and potential soil erosion on sloping terrain[62]. In addition to water infiltration at the soil surface, biopores also contribute to water percolation deeper in the soil profile[63]. Under saturated or near saturated conditions, large earthworm burrows (> 6 mm in diameter) in the subsoil act as preferential flow paths for water even when not continuous from the topsoil[63].

Since biopores allow water and solutes to be transported rapidly into deeper soil layers, they potentially have unwanted effects on nutrient leaching, as shown for the transport of nitrate through root channels[64]. Generally, slow percolation of water through the soil matrix allows P adsorption, whereas water and solutes transported through large biopores bypass the adsorptive capacity of the soil[65]. Thus, preferential flow through biopores can increase leaching of dissolved P[66]. However, the largest leaching losses of P in macropore flow were reported from soils with excessive topsoil P contents due to over-fertilization[57]. In conventional agriculture, preferential flow through biopores could also contribute to the transport of agrochemicals and potential contamination of natural groundwater bodies[67].

Root growth

The distribution of roots in soil is a main determinant in the ability of crops to acquire nutrients because the concentration of soluble nutrients in the liquid soil phase is typically low[68]. For this reason, soil structural features facilitating root growth are of particular interest in organically managed soils. The early observation that roots preferentially expand through biopores[13] has been confirmed by numerous studies[5,69,70]. Several reasons for this preference have been identified. First and foremost, roots follow biopores because they provide zones of reduced mechanical resistance[71]. This is of particular relevance because mechanical resistance has been identified as a major limitation to soil exploration by roots[72,73]. Root elongation is particularly slowed when stresses are exerted in an axial direction, which occurs when roots are growing through the bulk soil[74]. When growing through severely compacted soil zones, roots can potentially be deflected and buckle[75], which further delays root extension to deeper soil layers. Additionally, biopores are attractive for roots because they provide higher oxygen concentrations in the gaseous phase and higher nutrient concentrations in the solid phase (i.e., the pore wall) as compared to the surrounding soil[76]. Because of elevated oxygen concentrations, root respiration and root growth in biopores can occur at greater depths as compared to the bulk soil[77].

The importance of biopores for root elongation varies with soil properties. Whereas in comparatively compact subsoils, roots have been reported to grow predominantly in biopores[5,69], the share of roots in biopores did not exceed 25% in a Haplic Luvisol[78]. In the latter study, the percentage of roots growing in biopores was lower in the C horizon than in the denser Bt horizon. This result indicates that roots growing along biopores can eventually bypass compacted soil layers and re-enter the bulk soil in less compacted soil layers. Accordingly, root growth through biopores can facilitate the exploration of water and nutrients stored in the deep bulk soil. Soil strength and the angle of the biopores are crucial for the likelihood that a root re-enters the bulk soil from a biopore[79]. In a study by Hirth et al.[80] most roots of *Lolium perenne* L. were able to leave artificial biopores with an inclination of 40°, whereas the roots predominantly remained in vertical pores.

Acquisition of water and nutrients

The facilitation of root growth by biopores can increase the accessibility of water resources for crops. Gaiser et al.[81] demonstrated that the extraction of water from > 95 cm soil depth by spring wheat during a dry spell was increased when it was grown in field plots where the biopore density in the subsoil was increased by previous cultivation of perennial lucerne.

Biopores can facilitate the acquisition of nutrients from the subsoil via (1) increasing the root-length density in the bulk soil or (2) uptake of nutrients from the pore wall. The relevance of both processes largely depends on topsoil conditions. Low nutrient concentrations[82,83] and drought[84] have been shown to increase the percentage of nutrients taken up from the subsoil. Because the frequency of drought in some areas is expected to increase under global climate change[85], subsoil processes related to biopores could be of increasing importance in the future, particularly in organic production systems with a rather low nutrient availability in the topsoil.

The contribution of biopores to nutrient acquisition is not yet quantified. Nutrient acquisition from the bulk soil can only be increased by biopores if the soil conditions allow re-entry of roots growing through biopores into the bulk soil. At least for earthworm burrows, the properties of biopore walls can be considered to be favorable for nutrient uptake. Most importantly, the coatings of biopores typically can contain more nutrients than the surrounding soil, which has been reported particularly for nitrate[86,87], ammonium[88], phosphate and K[27,40]. Total carbon and organic carbon are enriched in the pore wall as well[89,90].

The walls of earthworm burrows have been identified as a hot spot of microbiological activity, as indicated by increased basal respiration, dehydrogenase activity and phosphatase activity[38,90,91]. Therefore, earthworm coatings potentially provide not only the nutrients deposited by feces and mucus of earthworms, but also nutrients mobilized from the solid phase by microbial activity. In addition, root activity can enhance weathering in the pore wall[92]. However, lack of root–soil contact in biopores much larger than the root's diameter, as well as clumping of roots in biopores, have been reported to be a major drawback of biopore benefits for crop performance[93,94]. On the other hand, under field conditions about 85% of winter barley or oilseed rape roots growing in biopores with a diameter of >5 mm did contact the pore wall—barley roots established the contact mainly by thin vertical roots, whereas rapeseed typically established the contact via lateral roots emerging from thick vertical main roots, growing centrally through the pore[44]. White and Kirkegaard[95] reported that wheat roots growing without direct contact to the pore wall frequently had root hairs contacting and entering the wall. Although precise quantification of nutrient uptake from biopores is still lacking, it is plausible that biopores contribute to the nutrient acquisition of crops, especially if they are coated with nutrient-rich earthworm excreta.

Managing Large-sized Biopores in the Subsoil

Biopore density can be influenced by the share of dicotyledons in the crop rotation because the roots of dicots generally have a higher proportion of thicker roots which are more capable of penetrating dense soil because they exert large radial pressures[96,97]. Hence, they are assumed to create more stable biopores than the roots of monocots[98]. Moreover, perennial root systems have the ability to create comparatively stable, continuous pore systems[99]. Taprooted ley crops commonly grown in organic crop rotations in temperate climates, such as grass–clover or lucerne, were repeatedly shown to increase macroporosity[100–103].

Likewise, catch crops with taproot systems can be used to create biopores. In this context, forage radish (*Raphanus sativus* var. *longipinnatus*) seems to be an appropriate crop because it is known to have a particular high penetration capability as compared with other catch crops such as oilseed rape or rye[104]. Root growth and yield of soybeans were greater following a combination of forage radish and rye as cover crops than following no fodder crop, probably because remaining root channels had provided soybean roots with low resistance paths to subsoil water[105]. Furthermore, forage radish grown as a cover crop was reported to benefit root penetration of following maize in compacted soil[106].

Density and—in particular—the quality of biopores, e.g., the nutrient contents of pore walls, can be also influenced by the activity of anecic earthworms. Anecic earthworms can create new pores even in compacted soil layers[2]. Moreover, anecic earthworms reuse existing burrows, which was reported for both juvenile individuals[107] and mature individuals of *L. terrestris* L.[108,109]. Specimens of *L. terrestris* can enter narrow pores and widen them because they can exert high radial pressures[110]. Such widening can increase the stability of pores because wider pores are less prone to compression than the narrower pores[111]. Furthermore, earthworms deposit fine-textured material in the pore wall[112] which results in increased packing density and stability of the pore wall. The populations of anecic earthworms can be increased by reducing the frequency and intensity of tillage[112,113]. Thus, any measures to increase the duration of soil rest are considered beneficial for promoting earthworm populations. Tillage also destroys the openings of vertical biopores to the surface and therefore diminishes the effectiveness of these pores in promoting water infiltration and gas exchange with the atmosphere. It has to be taken into account, that even after longer periods of soil rest, earthworm abundances will decrease drastically after the first tillage event. Nonetheless, the effects on subsoil structure generated during the period of increased population size and activity may remain, because biopores may be stable for decades[3,114]. Moreover, the time of tillage can have an effect on earthworm populations. For example, the abundance of *L. terrestris* was reported to be higher after spring cultivation as compared to autumn cultivation[115], probably due to the longer presence of crop residues on the soil surface. Furthermore, food quality parameters (such as C/N-ratio[116,117], polyphenol concentration[118] and texture[119]) were found to influence earthworm populations.

Other strategies for increasing earthworm populations in arable fields include the reduction of tillage depth and implementation of conservation tillage—or even no-till practices[120]. These measures have considerable effects on anecic earthworms; however, in organic agriculture they can be difficult to establish under Central European climates because of the importance of tillage for nutrient mobilization and weed suppression.

Conclusions

Based on the current state of research it can be assumed that a high biopore density will mostly result in beneficial effects on root growth and crop performance. The relevance of these effects can be particularly pronounced in organic production systems, where crops largely rely on nutrient acquisition from the solid soil phase with particular benefit from increased root-length density and the presence of hot spots for nutrient acquisition in the subsoil. Organic land-use strategies should take into account the consequences of cultivation on formation and maintenance of biopores and aim to increase number, stability and quality of biopores.

Managing biopores to facilitate access to water and nutrients follows the fundamental principle of organic farming. Crop production should be based on the living soil and on ecological processes. Moreover, a high density of biopores could facilitate the acquisition of water and nutrients particularly under conditions of drought, thus contributing to increased cropping system stability, another overall aim of organic agriculture. In 1943, Howard, one of the pioneers of organic agricultural research, stated that organic farmers should manage their soils after 'nature's methods of soil management'[121]. In this spirit, promoting the formation of biopores is a classic organic element of soil management.

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