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Review

Nutrient acquisition from arable subsoils in temperate climates: A review

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ABSTRACT

In arable farming systems, the term 'subsoil' refers to the soil beneath the tilled or formerly tilled soil horizon whereas the latter one is denoted as 'topsoil'. To date, most agronomic and plant nutrition studies have widely neglected subsoil processes involved in nutrient acquisition by crop roots. Based on our current knowledge it can be assumed that subsoil properties such as comparatively high bulk density, low air permeability, and poverty of organic matter, nutrients and microbial biomass are obviously adverse for nutrient acquisition, and sometimes subsoils provide as little as less than 10% of annual nutrient uptake in fertilised arable fields. Nevertheless, there is also strong evidence indicating that subsoil can contribute to more than two-thirds of the plant nutrition of N, P and K, especially when the topsoil is dry or nutrient-depleted. Based on the existing literature, nutrient acquisition from arable subsoils may be conceptualised into three major process components: (I) mobilisation from the subsoil, (II) translocation to the shoot and long-term accumulation in the Ap horizon and (III) re-allocation to the subsoil. The quantitative estimation of nutrient acquisition from the subsoil requires the linking of field experiments with mathematical modelling approaches on different spatial scales including Process Based Models for the field scale and Functional–Structural Plant Models for the plant scale. Possibilities to modify subsoil properties by means of agronomic management are limited, but 'subsoiling' – i.e. deep mechanical loosening – as well as the promotion of biopore formation are two potential strategies for increasing access to subsoil resources for crop roots in arable soils. The quantitative role of biopores in the nutrient acquisition from the subsoil is still unclear, and more research is needed to determine the bioaccessibility of nutrients in subsoil horizons.

1. Introduction

In mainstream agriculture supplying nutrients as fertilisers – predominantly in soluble form – to the topsoil is a standard practice to achieve high agricultural output. This procedure depends on annual inputs of resources and energy and has been identified as

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a non-sustainable method of crop production (Horrigan et al., 2002). In the future, decreasing resources e.g. of natural phosphate and potentially rising energy prices are supposed to result in increasing prices for mineral fertilisers (Cordell et al., 2009). Despite the urgent need to make new nutrient sources accessible for sustainable agriculture, one of the largest nutrient reservoirs – the subsoil – has been widely neglected by scientists in the past and remains largely unexplored. To date, there is still uncertainty about basic processes related to nutrient acquisition. Overall, the activity of roots (often limited by adverse soil structural features) is considered to be a key factor for accessing subsoil nutrients.

The precise quantification of nutrient availability and mobilisation as well as the prognosis of crop demands for nutrients and fertiliser application are still not reliable: Many studies have shown that even in soils poor in P or K, fertiliser applications often resulted in no yield increase (Schachtschabel, 1985; Jungk et al., 1993). This is partly because conventional soil analyses seldom assess nutrients delivered from the subsoil, i.e. N and P mineralised from organic compounds as well as the N, P and K amounts released from iron oxides, clay minerals or primary minerals. Hence, the potential contribution of long-term N, P and K release from subsoils to overall crop nutrition may have been underestimated. S, Ca, Mg and micronutrients stored in the subsoil are also supposed to contribute to crop nutrient supply, but very few data on subsoil specific mobilisation processes or uptake from the subsoil are available.

Long-term studies on nutrient balances, e.g. Carter and Gregorich (2010) for N, Gransee and Merbach (2000) for P and Heming (2004) for K, suggest that there is a need to establish the availability of nutrients stored in the subsoil. The relevance of the subsoil for nutrient acquisition by crops is considered to be exceptionally high when topsoils are dry or depleted in nutrients (e.g. Fleige et al., 1983; Kuhlmann and Baumgärtel, 1991). However, the subsoil's particularities – especially its structural heterogeneity – require a detailed view on the processes of nutrient acquisition involved at spatial scales from the level of clay size particles (<2 μm) to the soil profile (more than 1 m). The temporal scales that are relevant for nutrient acquisition from the subsoil range from decades to millennia (Fig. 1). In contrast to the loosened topsoil where mineralisation happens relatively fast and nutrients can be acquired from fertiliser applications, in the subsoil slower processes such as chemical weathering are comparatively more relevant for nutrient acquisition of crops.

This review outlines the current knowledge regarding those subsoil properties relevant for nutrient acquisition by crops and presents a conceptual model of nutrient acquisition from arable subsoils (Fig. 2). Corresponding to this concept, the review discusses the role of soil structure, root and microbial activity for nutrient acquisition and highlights the subsoil contribution to nutrient uptake, focussing on N, P and K. In order to quantitatively integrate the different processes, mathematical modelling becomes important. Thus, different approaches for modelling nutrient acquisition from the subsoil are also reviewed. Finally, we review new approaches for assessing nutrient acquisition from the subsoil and discuss strategies for influencing nutrient uptake from subsoil via agronomic management tools. Generally, the review only takes into account rootable, unconsolidated, mineral subsoils. It does not take into account consolidated bedrock material and consolidated subsoil horizons formed by mineral precipitation like calcretes or silcretes (Klappa, 1983; Sommer et al., 2006) or e.g. enrichment of Fe and Mn oxides as in Podzols (Lundström et al., 2000).

2. Subsoil properties

Roots of arable crops entering the subsoil, i.e. the soil beneath the Ap horizon, meet an environment remarkably different from the topsoil (i.e. the tilled or formerly tilled horizon). Table 1 lists bulk soil properties different in topsoil and subsoil layers focussing on loamy soils in temperate climates where a high proportion of the comparatively few studies on nutrient acquisition was undertaken. Contents of carbon and plant nutrients in the subsoil are lower than in the topsoil (see Table 1 for references). For instance, Salome et al. (2010) reported that C and N contents were 3.7 and 2.7 times lower

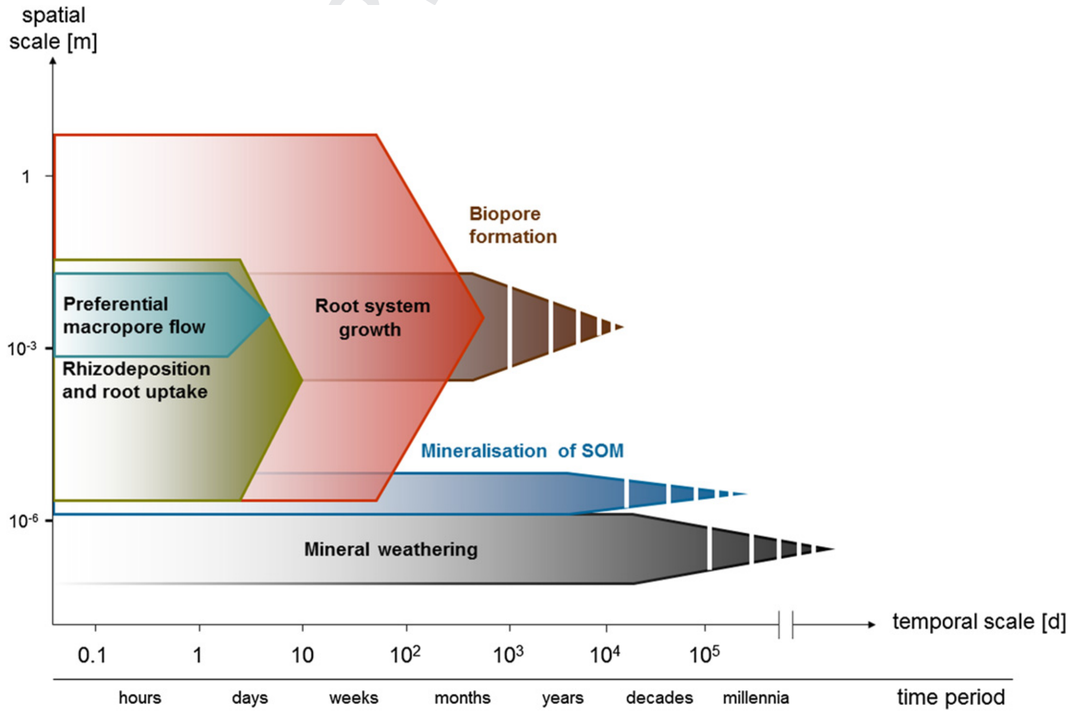

Fig. 1. Spatial and temporal scales of processes involved in nutrient acquisition from the subsoil.

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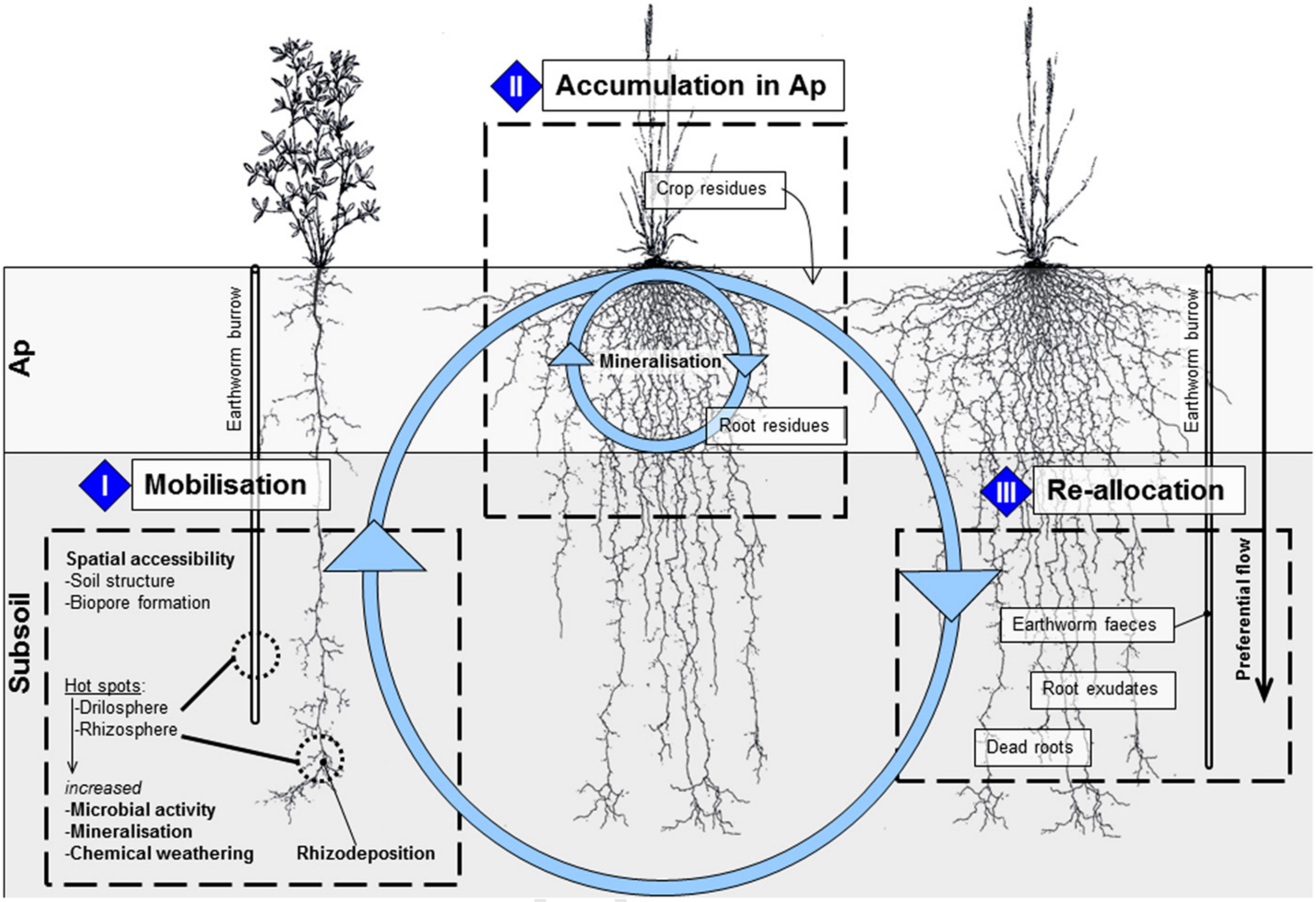

Fig. 2. A conceptual model of nutrient acquisition from the subsoil. Drawings of crops taken from Kutschera et al. (2009).

respectively in 80–100 cm soil depth than compared with the 5–10 cm soil layer (Table 1). However the total amount of organic matter and plant nutrients in the subsoil can be remarkable. Guo et al. (2006) have shown that within 20–200 cm subsoil depth more than twice the amount of organic C may be stored than in the 0–20 cm topsoil layer. In general, the spatial accessibility of the less mobile P and K in the subsoil is lower than in the topsoil. Compared with the Ap horizon, only a relatively small proportion of the subsoil volume actively contributes to plant nutrition, because root length densities are generally low. For instance, Köpke (1979) reported the rooting density of wheat to be three to four times lower than in the Ap horizon (Table 1). Subsoil aggregates are often not rooted and the distances between neighbouring roots growing outside macropores are larger than in the topsoil (Lipiec and Hatano, 2003). Hence, nutrient acquisition from the subsoil is influenced by root morphology and architecture, as well as by rhizosphere extension and various biochemical strategies of the crop effective for nutrient mobilisation (Richardson et al., 2009).

In contrast to the Ap horizon, where soil structure is frequently disturbed by tillage practices, in the subsoil, networks of macropores (Beven and Germann, 1982) can persist for longer periods of time. Because of the higher bulk density of the subsoil compared with the Ap horizon (Nissen, 1999, Table 1), these subsoil structures markedly influence water and oxygen transport, root growth, microbial activity and community composition, and hence nutrient release from the solid phase, i.e. mineral or organic soil compounds (Jakobsen and Dexter, 1988; Stirzaker et al., 1996; Dexter et al., 2004). Macropores may be grouped into (a) round-shaped biopores created by root growth and activity by the soil fauna and (b) cracks and fissures as induced by swelling and shrinkage (Oades, 1993; Bronick and Lal, 2005; Horn and Peth, 2011). The number of earthworm burrows in the subsoil can be 9-fold higher than in the Ap (Ehlers, 1975, Table 1). In the subsoil, the drilosphere defined as a 2 mm wide zone around earthworm burrows (Bouché, 1975; reviewed by Brown et al., 2000) represents a microsite often enriched in soil organic matter and nutrients and with a generally higher accessibility for roots.

3. A conceptual model of nutrient acquisition from the subsoil

In the subsoil, nutrients are less equally distributed than in the topsoil. While in the bulk subsoil the conditions for biological activity – and root growth in particular – are generally adverse, the drilosphere is considered as a potential hot spot for nutrient acquisition. Furthermore, soil water as a mediator for solute transport plays an important role in every process component of nutrient acquisition, particularly in the subsoil as the distances between roots and nutrient sources may be greater. In general, three main process components can be discerned (Fig. 2).

I. Nutrient mobilisation in the subsoil: the impact of root and microbial activity on nutrient spatial accessibility and mobilisation from the solid phase (chemical weathering, desorption and mineralisation).

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Table 1
Comparison of bulk topsoil and bulk subsoil properties shown exemplarily for some soil field sites in temperate climate. Mean values indicate arithmetic means except for values marked with an asterisk (*), indicating geometric means.

Soil property	Topsoil			Subsoil			Soil type/soil texture class	Reference
	Depth (cm)	Mean	Range	Depth (cm)	Mean	Range		
Bulk density (g dm^{-3})	0–30	1.45	1.19–1.72	>30	1.56	1.39–1.90	13 sites (Luvisol, Chernozem, Cambisol, Fluvic Cambisol, Gleysol, Stagnic Anthrosol, Eutric Cambisol)	Nissen (1999)
Total pore volume		44	34–54		40	26–47		
Air capacity (vol.%)		8	1–20		4.8	0–13		
Air permeability ($cm^2 * 10^{-8}$)		11.0*	1.4–66.2		10.8*	0.3–70.5		
Saturated hydraulic conductivity (cm d^{-1})		37.4*	1–575		16.4*	<1–207		
Cohesion (kPa)		14	0–29		18.7	4–35		
Angle of internal friction (°)		34	25–41		32.9	19–42		
O_2 concentration (%)	15	20.52		46	20.33		Arable land, manured	Lal and Shukla (2004) based on Russell and Appleyard (1915)
CO_2 concentration (%)		0.34			0.50			
Number of earthworm burrows m^{-2} in tilled soil								
Diameter 2–5 mm	20	60		60	174		Grey-brown podzolic soil (Typudalf)	Ehlers (1975)
Diameter 5–8 mm		18			165			
Diameter 8–11 mm		1			9			
C (mg g $soil^{-1}$)	0–22/28		11.6–12.3	22/28–45		3.6–7.7	Haplic Phaeozem	Wiesenberg et al. (2006)
				45–70		2.2–5.8		
C (mg g $soil^{-1}$)	5–10	12.56		80–100	3.39		Eutric Cambisol/Luvisol	Salome et al. (2010)
N (mg g $soil^{-1}$)		1.23			0.43			
C/N		10.82			7.94			
Total P (mg kg^{-1} soil)	0–20		558–1048	75–100		261–483	Cambisol from loess	Schwertmann and Huith (1975)
P_2O_5 lactate soluble (mg kg $soil^{-1}$)			140–550			10–20		
P lactate soluble (mg kg^{-1} soil)	0–30		70–130	30–100		5–40	21 sites (Luvisols from loess)	Schachtschabel and Beyme (1980), Steffens (1984), Werner et al. (1988)
K_2O lactate soluble (mg 100 g^{-1} soil)	0–20		60–138	75–100		17–22	Cambisol from loess	Schwertmann and Huith (1975)
K exchangeable (mg kg^{-1})	0–25		60–239	40–70		15–149	8 sites (Regosol, Umbrisol, Phaeozem, Cambisol)	Andrist-Rangel et al. (2006)
K aqua regia (g kg^{-1})	0–25		1.61–10.80	40–70		2.18–12.29	8 sites (Regosol, Umbrisol, Phaeozem, Cambisol)	Andrist-Rangel et al. (2006)
Redox potential (mV)	0–30	339	253–415	30–60	323	235–415	Luvic Chernozem	Bohrerova et al. (2004)
Microbial biomass (% of extractable PLFAs)	0–25	65		26–200	35		Mollisol	Fierer et al. (2003)
Microbial biomass (μg g^{-1} soil)	5–10	121.3		80–100	28.8		Eutric Cambisol/Luvisol	Salome et al. (2010)
Microbial biomass (mg C 100 g $soil^{-1}$)	0–30	11.63		100–130	7.78		2 sites (Iowa clay Michigan sand)	Taylor et al. (2002)
		7.77			2.36			
AMF spore abundance (number of spores g^{-1} soil) in a maize field	0–10		7–14	50–70	1.3		2 sites (Calcaric Regosol, Haplic Alisol)	Oehl et al. (2005)
Rooting density (minirhizotron; maize roots cm^{-2})	10	2.25		80	1.13		Sandy loam	Liedgens and Richner (2001)
Rooting density (profile wall, cm wheat roots cm^{-3} soil; 3 sampling dates; means of 3 cultivars)	0–30	0.29		30–100 (max depth)	0.07		Luvisol from loess	Köpke (1979)
	0–30	0.39		30–150 (max depth)	0.12			
	0–30	0.83		30–190 (max depth)	0.21			

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II. Nutrient accumulation in the Ap horizon: turnover and long-term accumulation of nutrients acquired from the subsoil and translocated in the shoot and root systems, predominantly as a result of litter mineralisation in the Ap horizon.

III. Re-allocation of nutrients and organic C into the subsoil: creation of hot spots for increased root and microbial activity in the subsoil via downward transport of easily available organics and nutrients as well as nutrient accumulation in the drilosphere of the subsoil, primarily as a function of root transport, root decay, earthworm activity and preferential flow through biopores.

Due to the multitude of processes at various temporal and spatial scales involved (Fig. 1) and due to the complexity of interactions, the process components described above can hardly be quantified precisely by direct measurements, but must be estimated by mathematical simulation. For this reason, options for mathematical modelling of the process components are reviewed at the end of this section.

3.1. Nutrient mobilisation

In light of the comparatively scarce, heterogeneous subsoil root systems, nutrient mobilisation in the subsoil starts with spatial access to nutrients for roots and microorganisms. Regarding the subsoil structure, macropores could be of particular interest since they represent preferential pathways for root growth and transport of water, solutes and gases. In contrast, the bulk subsoil is generally less permeable for roots, gases and liquids. At least for the walls of macropores formed by earthworms, comparatively high contents of organic matter, presence of active roots and oxygen can promote microbial activity and will thus facilitate nutrient mineralisation from the solid phase (Kuzyakov et al., 2007). In this view, biopore formation in the subsoil might largely interact with other processes of nutrient mobilisation, such as root growth, rhizodeposition, microbial activity and nutrient mineralisation from mineral and organic sources.

3.1.1. Spatial accessibility: soil structure dynamics and macropore formation

Soil structure determines the rootability as well as the distribution of gases, water, solutes and organisms in soils, thus influencing nutrient accessibility and nutrient mobilisation processes. In subsoils the lack of inversion and/or mixing and loosening by tillage leads to a more stable but rather heterogeneous environment compared with the Ap horizon where repeated homogenisation takes place. As a consequence, soil structure and associated physical properties in subsoils are more ‘mature’ than in topsoils. Subsoils are structurally more ‘diverse’ than topsoils with a particular site and management specific association of macropores of different origins. Subsoil specific pore architectures influence soil functions in various ways. Plant roots, earthworms and other macrofauna create elongated pores with cylindrical shapes and smooth curved surfaces (Oades, 1993), thus altering soil structure on spatial scales of up to several cm (Fig. 1). To date, it is not completely clear at which temporal scales the processes of biopore formation occur, but we assume that, although roots can penetrate the subsoil within a few weeks, the development of a stable biopore system requires interaction of root growth and earthworm activity over several years (Fig. 1). Biopores allow preferential water flow and rapid solute transport in the soil profile even if the soil is not fully saturated (Jarvis, 2007; McGrath et al., 2010). On the other hand roots exert mechanical stresses at the root tip during root elongation (Bengough et al., 2006) resulting in a reorientation of soil particles and an increase in bulk density around the root (Hinsinger et al., 2009). Such compression effects are also observed for earthworm burrows (Lee, 1985). Hence, the lateral transport of air and water is modified around biopores, which in turn influences nutrient accessibility and fluxes.

Pathways for preferential flow – including biopores – can be stable at least for decades (Hagedorn and Bundt, 2002). Cresswell and Kirkegaard (1995) found relationships between the morphology of the root system and specific physiological and morphological adaptations of the roots and the development of macropore systems. However, roots also transmit hydraulic stresses within the soil–plant–atmosphere continuum (SPAC) to the soil and create gradients by water and nutrient uptake. If the internal soil strength is smaller than the exerted hydraulic stress, further soil heterogenisation and aggregate formation due to cracking occur (Bruckler et al., 1991; Lafolie et al., 1991; Oades, 1993). In addition roots and microbes secrete extracellular polysaccharides (EPS) that locally bind solid particles into more or less stable aggregates (Cheshire, 1979; Dorioz et al., 1993; Rillig et al., 2002). During the degradation of root residues, diverse substance groups such as carbohydrates, phenolic molecules and lignin are released enhancing soil aggregation (Bronick and Lal, 2005; Majumder and Kuzyakov, 2010). They continually interact with abiotic factors which are just as important for subsoil structure dynamics. In general, rhizodeposition can affect soil aggregation on spatial scales from a few μm to more than 1 cm (Fig. 1).

Structural subsoil characteristics such as high soil density may limit root elongation, for example if (i) oxygen diffusion to root tips is insufficient, (ii) water availability is insufficient for root water uptake, or (iii) mechanical impedance of the soil is too high (Taylor and Ratliff, 1969; Blackwell and Wells, 1983; Sharp et al., 1988; Horn, 1990, 1994; Whalley et al., 1995; da Silva et al., 1997; Bengough et al., 2006). Thus, subsoil features an outstandingly heterogeneous structure, with many implications for processes of nutrient acquisition.

3.1.2. Root growth and rhizodeposition

Rooting density and spatial distribution of roots in the heterogeneous subsoil play an essential role for nutrient and water uptake (see reviews by Hinsinger et al., 2009; Hodge et al., 2009). Size and architecture of the root system as well as rhizosphere extension determine the plant’s ability to access water and nutrients. These factors limit plant growth and thus crop yield in many agricultural ecosystems (Lynch, 1995). Furthermore, roots provide substrates for microorganisms (Blagodatskaya et al., 2009). As outlined (Section 3.1.1), roots participate in soil structure formation and, in turn, the soil structure largely determines the extent and orientation of root systems.

In the subsoil, plant roots have been reported to grow predominantly in macropores (Böhm and Köpke, 1977; Watt et al., 2006) formed either as a consequence of biological activity (old root channels and earthworm burrows) or by physical processes (swelling and shrinking). Pierret et al. (1999) found that about 80% of all subsoil roots grow in the direct vicinity of macropores. Zones of high mechanical resistance represent one of the most common physical limitations to soil exploration by roots (Unger and Kaspar, 1994; Hoad et al., 2001). Lower mechanical impedance, presence of oxygen and nutrients are the main factors for preferential growth of roots in macropores (Stewart et al., 1999). The relevance of macropores enabling crops to access subsoil resources was also demonstrated by McKenzie et al. (2009). They used a nylon mesh sheet buried horizontally in the soil which allowed root growth into deeper soil layers only through previously inserted holes which mimicked macropores in a compacted soil layer. In this study, leaf area index and plant height of five barley genotypes increased with increasing number of holes in the restricting mesh during a dry summer season.

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Vertically oriented macropores provide preferential pathways for unimpeded root growth. Once a root enters such a pore, it will grow along it until the angle of the channel and the penetration resistance of the surrounding soil may allow a re-entry to the bulk soil (Bengough, 2003). Re-penetration to the bulk soil has been reported for roots growing at a 40° angle in biopores (Hirth et al., 2005).

Living roots growing in biopores in close contact with the pore wall on the one hand contribute to enrichment of organic matter in the drilosphere and on the other hand deplete nutrients from the drilosphere (Jones et al., 2004). So far, it remains unclear to which extent the nutrients stored in the drilosphere can be used, particularly in the subsoil. Typically, roots growing in earthworm burrows are supposed to benefit from nutrient-rich inner wall coatings (Graff, 1971), but in case of a limited direct contact area between roots and the pore wall, as reported by White and Kirkegaard (2010), the drilosphere as a nutrient resource would at least partly remain unexplored. However, White and Kirkegaard (2010) have shown that in these cases root hairs can establish contact with the pore wall. Furthermore, mycorrhizal hyphae that increase the uptake surface by about two orders of magnitude could close the gap between roots and larger macropores, although this has not been verified yet. Since lack of oxygen limits nutrient uptake (Stępniewski and Przywara, 1992), macropores have to be considered as preferred areas of nutrient uptake. Concerning the chemical nutrient availability from the pore wall, Eich-Greatorex and Strand (2006) noted that lower amounts of easily weatherable minerals (e.g. chlorite and biotite) are present in the vicinity of root-filled pores and suggested enhanced weathering in the pore wall caused by root activity.

Physical, chemical and biological soil conditions are influenced via rhizodeposition, i.e. exudation of organic compounds (Curl and Truelove, 1986; Barber, 1995; Kuzyakov, 2002) and root border cells. Rhizodeposition as a factor of nutrient acquisition is presumed to be more important in the subsoil than in the topsoil because of lower substrate availability and consequently lower microbial activity. A field study with maize Rasse et al. (2006) showed that about one third of the C that has been freshly deposited into the soil was located underneath the plough layer. These authors suggest that fine root activity, bioturbation, and dissolved organic carbon (DOC) transport influence the distribution profile of recently deposited C. From topsoil-studies it is known that rhizodeposits compared with stabilised soil organic C are the preferred C substrates for microbial utilisation (Yevdokimov et al., 2006; Blagodatskaya et al., 2009). If this holds true for the subsoil as well, we assume that the rhizosphere can be a hot spot of microbial activity in the subsoil. Therefore the root and microbial mediated weathering in the subsoil is relevant with regard to long-term delivery of nutrients for ecosystems, though better quantification of such processes in the subsoil is still needed for a better understanding of the overall nutrient dynamics in the subsoil.

Nutrients – especially P – can be additionally mobilised by arbuscular mycorrhiza (AM), which are able to develop hyphae reaching up to several centimetres away from the root surface (Allen, 1991). The contribution of AM to the plant P uptake from organic and inorganic soil P was reviewed by Read and Perez-Moreno (2003), Vance et al. (2003), and Bucher (2007). Mycorrhizal abundance seems to decrease with increasing soil depth (Oehl et al., 2005; Yang et al., 2010). The rate of root infection by AM has also been reported to decrease substantially below a soil depth of 40 cm (Jakobsen and Nielsen, 1983) but related research is again scarce compared with topsoil studies. However, a few *Glomus* and *Scutellospora* species were found to occur predominantly or even exclusively in the subsoil (Oehl et al., 2005), indicating that specialised AM species allow nutrient mobilisation also in the subsoil. Considering the structural subsoil features that hinder roots to extensively explore the bulk soil, it is still unclear whether mycorrhizal fungi play a significant role in the nutrient mobilisation from the subsoil.

3.1.3. Accessibility of soil organic matter and implications for microbial activity and dynamics in community structure

Contents of available C and N in the subsoil are normally significantly lower than in the topsoil (Qualls and Haines, 1992) and as a consequence, also the microbial biomass (Vinther et al., 1999; Taylor et al., 2002). In a comparison of 5–10 and 80–100 cm soil depth levels, Salome et al. (2010) found the microbial biomass to be 4.2 times lower in the deeper layer (Table 1). With respect to total soil organic matter, the percentage of stable organic compounds increases with soil depth (e.g. Rethemeyer et al., 2005). Probably, this is due to the lack of fresh organic C as an energy source (Fontaine et al., 2007), stable bonding between organic and mineral particles (Kaiser et al., 2002), inaccessibility (physical occlusion) of organic carbon deposited in very small pores of the bulk soil and thus lower microbial activity (Six et al., 2004; Kinyangi et al., 2006). Reduced decomposability and increased residence time of organic matter in the subsoil as compared with the topsoil were reported by Paul et al. (1997) and Rumpel et al. (2002). Spatial heterogeneity of C content, respiration and microbial communities are greater in the subsoil than in the topsoil and physical separation between substrate and decomposer can contribute to the stabilisation of OM in the subsoil (Salome et al., 2010).

It has been postulated for a long time that microbial communities living in subsoils are simply diluted analogues of the topsoil populations and exhibit minimal differentiation. Hence, it was argued that characteristics and properties of microbial processes in subsoils should be basically similar to those occurring in topsoils. Zvyagintsev (1994) was one of the first stating that deeper soil horizons may contain specialized microbial communities adapted to this environment. This assumption was substantiated 8 years later in a study by Fierer et al. (2003) showing that the number of individual phospholipid fatty acids (PLFAs), which they used as a proxy for microbial diversity, decreased with increasing soil depth. Whereas topsoils were dominated by PLFA from Gram-negative bacteria, fungi and protists, in deeper soil layers indicator PLFAs for Gram-positive bacteria and actinomycetes were highly abundant. Only approximately 35% of the total microbial biomass within the top 2 m of the soil profile was determined beneath 25 cm soil depth. Major parts of this pioneering study were confirmed by Ekschmitt et al. (2008), who also demonstrated a steep gradient of bacterial and fungal biomass from the topsoil to subsoil. All authors explained this reduction of microbial biomass with less availability of carbon and other nutrient sources in deeper soil layers. Even abundance of anaerobic bacteria decreases with soil depth, as determined via composition of glycerol dialkyl glycerol tetraether lipids as biomarkers of intact cell membranes of anaerobic bacteria (Weijers et al., 2010). So far an increase of certain functional groups in deeper soil layers has been reported for ammonia oxidising archaea only (Leininger et al., 2006), indicating fast turnover rates of available ammonia in subsoils.

A number of studies on the survival of typical microbes colonising nutrient rich topsoil habitats, like Pseudomonads or Enterobacteriaceae, which are occasionally transported into the subsoil through earthworm burrows, indicate that those microbes cannot tolerate the conditions in deeper soil layers (e.g. Joergensen et al., 1998). Very few authors have postulated that microbes in subsoils may play an important role for soil formation (e.g. Bezdicek et al., 2003) and ecosystem biogeochemistry. Most studies in this area are related to the question, whether denitrification plays a major role for providing electrons for reduction of organic material.

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However, the results published so far are not very clear. Murray et al. (2004) examined the potential of the subsoil to denitrify nitrate under anaerobic conditions in a laboratory incubation experiment. Both topsoil and associated subsoil were supplied with nitrate and either glucose, starch or cellulose. The subsoil supported low amounts of microbial activity and responded to the glucose treatment only. The N_2O production from the subsoil amended with glucose was less than 20% of that measured in the topsoil. This result indicates that the denitrifying microbial community of the subsoil is partly limited by the presence of readily available C sources (McCarty and Bremner, 1992; Clough et al., 2005). In contrast, Fangueiro et al. (2010) demonstrated higher N_2O production rates and an earlier start of denitrification from deeper soil layers after the application of slurry compared to topsoils. As a reason they postulated lower availability of oxygen in deeper soil layers. These contradicting data clearly indicate that there is a need to improve our understanding on the ecophysiology of functional units in subsoil systems. For example operon structures and promoter regions of microbes living in the subsoil catalysing nitrite reduction, NO reduction and N_2O reduction might differ from those colonising topsoils, resulting in different levels of control of denitrification in different soil compartments. In addition there have been speculations as to whether a large portion of denitrifiers colonising subsoils lack N_2O reductase *nosZ*, which might explain high production rates of N_2O from subsoils.

3.1.4. N, P and K mobilisation from mineral and organic compounds

3.1.4.1. Nitrogen. In the subsoil, N as well as other nutrients can be mobilised from organic compounds. In general, little is known about the kinetics of nutrient release from organic C pools in the subsoil, but in the light of increased residence time of organic matter in the subsoil due to reduced bioaccessibility (see Section 3.1.3) it can be assumed that there is a lower rate of nutrient release from organic matter by microbial decomposition in the subsoil as compared to the topsoil. Also the racemisation of protein-bound amino acids in the subsoil suggests that they are not accessible to the soil microbial community (Amelung, 2003).

Apart from N mineralisation of organic matter, in the subsoil special attention has to be paid to specifically bound NH_4^+ deposited in the interlayers of 2:1 clay minerals. This N fraction amounts to 150 and 850 mg kg^{-1} soil at agricultural sites (Schachtschabel, 1961; Scherer and Mengel, 1979). Its share of the total-N content in the topsoil varies between 3 and 14% and increases in general with increasing soil depth (Scherer, 1993), up to 36% of total N (Paramasivam and Breitenbeck, 1994). This is partly due to higher contents of specifically bound NH_4^+ in the subsoil as well as to the decrease of the contents of organically bound N (Dressler and Mengel, 1986). The mechanism of NH_4^+ release from clay mineral interlayers is still not completely understood. However, it is assumed that this process is controlled by diffusion and generally occurs when the NH_4^+ concentration in the vicinity of the clay minerals is low (Nieder et al., 2011). According to Scherer and Ahrens (1996) plant roots deplete the NH_4^+ concentration of the soil solution in the rhizosphere and thus promote the release of specifically bound NH_4^+. Moreover, the release of NH_4^+ is governed by the K^+ concentration in soil solution. Under field conditions, continuous uptake of NH_4^+ and K^+ ions by roots may reduce concentrations of both ions and therefore, diminish the blocking effect of K^+ on the release of NH_4^+ (Scherer, 1993). Under conditions of a substantial depletion of exchangeable NH_4^+ in the mycorrhizal sphere an effect of mycorrhiza on the mobilisation of specifically bound NH_4^+ might be found (Scherer and Frost, 2004). Furthermore, an enhanced NH_4^+ flux from the clay mineral layers is to be expected especially in the subsoil, where, caused by lower microbial activity, lower N mineralisation from organic matter and consequently, lower NH_4^+ concentrations in the soil solution prevail. Mobilisation of specifically bound NH_4^+ is closely related to N uptake by plants. Mengel and Scherer (1981), who investigated this N fraction throughout the growing season, reported that the content of specifically bound NH_4^+ in the top 60 cm dropped from February to May by about 18%. In the deeper soil layer the depletion occurred in a later period, which was in accordance with the root growth of the plants at this depth. Another important factor influencing the availability of specifically bound NH_4^+ is the soil water content. Under wet conditions clay minerals may expand, increasing the distance between the unit layers and thus facilitating the release of NH_4^+ ions from the interlayers. If the topsoil dries out during the summer, the N demand of plants may be at least partially (i.e. about 35–40%) covered from the subsoil by the release of specifically bound NH_4^+ (Mengel and Scherer, 1981). The phenomenon of temporary fixation and release of added fertiliser NH_4^+ may contribute to retarding nitrification and thus to reducing N losses from the soil–plant system via NO_3 leaching and denitrification. In maritime temperate climates, N leaching occurs frequently over winter as a consequence of rainfall and low N uptake by plants. Nieder et al. (2011) observed that in these climates the ammonium fixation capacity in the soil layer from 0 to 90 cm also reaches the maximum during the winter period. Therefore the extent of N leaching may partly depend on the NH_4^+ fixation capacity of the soil.

3.1.4.2. Phosphorus. The overall proportion of P in the subsoil ranges from 25 to 70% of the total P determined in the profile (e.g. Schwertmann and Huith, 1975; Godlinski et al., 2004) but little is known about P acquisition from the subsoil, regardless of the P form. To date, the predominant number of studies on P acquisition focused on topsoil or was conducted as pot experiments, mainly due to the lack of adequate tracer techniques for field studies. Weathering from primary minerals is probably a principal process responsible for P release in the subsoil. At present it cannot be predicted precisely, but a review by Newman (1995) suggests a P release through weathering up to 5 kg P ha^{-1} y^{-1}, depending on the parent rock material. Direct evidence is lacking for this number and the author did not specifically differentiate between surface and subsurface soil weathering, but since the subsoil comprises the larger amounts of unweathered primary minerals, it seems reasonable to assume that the P release from soil weathering largely affects P nutrition from the subsoil.

Generally, the content of inorganic P (P_i) decreases in the long-term due to weathering and subsequent plant uptake, whereas the contents of occluded P and organic P (P_o) contents increase due to fixation processes and biological turnover (Crews et al., 1995; Turner et al., 2007). The rate of P_o mineralisation can be far lower than the physico-chemical release of P_i (Oehl et al., 2004). Nonetheless, P_o can be of outstanding importance in the subsoil, at least in the drilosphere (Kuczak et al., 2006). Turner et al. (2005) pointed out that there is an urgent need to elucidate the biological origin and relevance of different P_o pools.

With increasing P limitation of the ecosystem, the relevance of P mobilisation from organic matter by mycorrhizal fungi increases (Read and Perez-Moreno, 2003). The plants' and AM strategies to access P_o were reviewed by Vance et al. (2003) and Bucher (2007), but many questions remain open, especially for subsoils. In agricultural ecosystems, the subsoil may considerably contribute to P nutrition, especially when topsoils are dry or P depleted (Garz et al., 2000).

Plants have been identified as 'P carriers' into the subsoil since high amounts of P_o, especially under high supply of organic fertilisers, are translocated into the subsoil via the root system (Oehl et al., 2002; Franchini et al., 2004). This heterogeneous nutrient deposition via the roots may influence the nutrient supply to the

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subsequent crops (Werner et al., 1988; Oberson et al., 1996). Decomposition of roots may influence P availability in the subsoil (Campbell et al., 1993). The mineralisation of dead biomass from both plant and microbes may significantly contribute to P nutrition (e.g. Di et al., 1997; Oehl et al., 2001; Turner and Haygarth, 2001). Amelung et al. (2001) found that there are forest and steppe soils where the P_o composition of the 0–10 cm soil layer does not differ significantly from that of the 40–50 cm soil layer. In forest soils, the organic P forms comprised mainly orthophosphate di-esters in the organic surface layers but in the mineral horizons orthophosphate monoesters dominated the chemical composition of extractable P_o (Möller et al., 2000). Yet, the P_o dynamics under the specific subsoil conditions are still poorly understood, and results of ^{31}P NMR analyses may still be biased by different extractability of P_o in surface and subsurface soils (Amelung et al., 2001).

The interactions of spatial accessibility and chemical availability of subsoil P for plant roots have not yet been revealed in detail. Nevertheless, it seems reasonable that biopores can have an important impact on P allocation and accessibility for roots in subsoil horizons.

3.1.4.3. Potassium. The kinetics of K release from the subsoil solid phase is closely linked to the type of association between K and the soil minerals as well as the type of parent material and soil texture. Organic matter is hardly involved in K mineralisation as K is present as a free ion in plant tissue, unlike P and N which are chemically bound (Römheld and Kirkby, 2010). In most agricultural soils, phyllosilicates are more relevant for K release than feldspar (Andrist-Rangel et al., 2006). From soils with a fine texture, i.e. with a high percentage of clay minerals, up to 35–70 kg K ha^{-1} a^{-1} can easily be released from the solid phase; whereas in soils with coarse texture, comparatively lower release rates are to be expected (Simonsson et al., 2007). In general, K release can result from the interchange of K from interlayers caused by cations with higher hydration energy, leading to expanded layers and to conversion from illite to vermiculite and finally smectite (Niederbudde and Fischer, 1980; Tributh et al., 1987; Hinsinger and Jaillard, 1993; Hinsinger et al., 1993; Wang et al., 2000; Moritsuka et al., 2004). The release of K from interlayers of illite is frequently considered an equilibrium reaction, which depends on K concentration in the soil solution, the number and accessibility of sorption sites, and the concentration of competing ions (Geelhoed et al., 1999; Kirk, 2002). Plants control water dynamics, weathering and the chemistry of weathering solutions (Lucas, 2001). This is of particular relevance for the subsoil as soil solution equilibrium is not altered by fertiliser application.

Roots can actively excrete H^+ which exchanges for other cations (K^+, NH_4^+, Ca^{2+}, Mg^{2+}) and thus maintains charge balance and drives the proton motive gradient across the plasma membrane. Concentration of individual ions can be increased or decreased in relation to bulk soil depending on the balance of ion transport to the root surface by mass flow and diffusion and the uptake capacity of the root (Hinsinger et al., 2009). The latter is a function of topsoil–subsoil feedback regulation (see Section 3.2). In the literature large differences in soil K concentration between rhizosphere and bulk soil have been reported (Claassen and Jungk, 1982; Moritsuka et al., 2004). However there is a lack of information on concentration gradients in soil solution and its temporal dynamic which can be very strong (Vetterlein and Jahn, 2004). It is well established that plants can induce release of interlayer ('non-exchangeable') K in the rhizosphere (Springob and Richter, 1998a). Under debate is the lower threshold K concentration which enables K release from interlayers (Claassen and Jungk, 1982; Hinsinger and Jaillard, 1993; Springob and Richter, 1998b; Moritsuka et al., 2004) and how this threshold is altered by the presence of other cations like Ca^{2+}, Mg^{2+} (Lumbanraja and Evangelou, 1990; Evangelou and Lumbanraja, 2002) and NH_4^+ (Scherer and Ahrens, 1996).

There is some evidence from field studies with corn, showing that vermiculite minerals were particularly concentrated near or at the surface of roots (Kodama et al., 1994). However, the authors point out, that this is no proof that plant induced vermiculitisation occurs in the rhizosphere. Vermiculite might have been simply accumulated by precipitation from suspension as this went through root channels.

As K uptake by plants is higher in the topsoil compared to the subsoil the general expectation is that illite content would decrease with soil depth and *vice versa* for vermiculite (Barré et al., 2007). In fact most of the long-term field trials investigated, mostly on forest and grassland sites, show the opposite and this can be explained by 'biocycling' or rather 'plant cycling' in the nutrient uplift theory (Tice et al., 1996; Jobbágy and Jackson, 2001; Barré et al., 2007). According to this theory K taken up by roots in the subsoil is transported to the shoot and through litter fall enters into the topsoil K pool. Barré et al. (2007) pointed out that as long as the balance between K translocation and plant uptake is positive, which is the case for many forest and grassland ecosystems, a gradual increase of illite in surface layers will occur. If the balance is negative as it was shown for a corn cropping system by Velde and Peck (2002) the amount of 'illite like' layers in topsoil decreases. The turning point depends not only on the amount of K exported from the system by harvest or leaching, but also on root architecture and subsoil accessibility.

3.2. Nutrient translocation to the shoot and long-term accumulation in the Ap horizon: relative contribution of subsoil to plant nutrition

Considerable amounts of N, P and K that have been absorbed by the roots from the subsoil are translocated to shoots and topsoil roots. In case they are not removed during harvest, they are deposited in the topsoil as residues, mineralised and available for nutrient uptake by following crops or dislocated back to the subsoil by leaching or soil biota activity. The process of nutrient accumulation in the topsoil as a consequence of litter fall and belowground remobilisation of root biomass has been termed as 'plant cycling' (see Section 3.1.4). Jobbágy and Jackson (2001) stated that plants exert a dominant control on the vertical distribution of the most limiting elements for plants. The potential of the subsoil for the nutrition of agricultural crops and thus also nutrient reallocation within the topsoil has been shown by numerous studies (Table 2).

The amount of N taken up from subsoil and the relative contribution of subsoil to total N uptake varies considerably with site and weather conditions as well as agricultural management. In an average of 22 sites (deep loess grey podsolic soils only) Kuhlmann et al. (1989) determined a subsoil contribution of about 1/3 to the total N uptake of winter wheat (Table 2). The distribution of N in the soil profile affects N uptake from the subsoil: Kuhlmann et al. (1989) demonstrated that unfertilised winter wheat took up 152 kg N ha^{-1} from a subsoil rich in N, whereas winter wheat fertilised with 170 kg N ha^{-1} took up only between 31 and 39 kg N ha^{-1} from subsoils containing less N. The amount of N taken up from the subsoil and deposited in the Ap finally depends also on the crop yield and thus the amount of crop residues.

The significance of the subsoil contribution to P uptake by plants increases with decreasing P contents in the topsoil. Before topsoils were extensively fertilised with P, Murdock and Engelbert (1958) proved by means of ^{32}P tracer methods, that the subsoil substantially contributed to P nutrition of maize. By replacing topsoil with soil substrates of defined P content, Kuhlmann and Baumgärtel (1991) determined that the subsoil delivered about 37–85% of

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Table 2
Contribution of subsoil to nutrient uptake by crops. Values indicate arithmetic means. Maximum and minimum values are shown in parentheses.

Nutrient	Soil	Crop	Fertilisation	Experimental years	Subsoil depth under study (cm)	Contribution of subsoil to nutrient uptake		Reference
						kg ha^{-1}	% of uptake	
N	Luvisol from loess (average of 22 sites)	Winter wheat	None	1	30–90		25	Kuhlmann et al. (1989)
					90–150		8	
					30–150		33 (9–75)	
	‘Deep clay loam’	Winter wheat	None	5	50–120	(21–62)		Haberle et al. (2006)
	‘Chernozem soil on loess’			3	50–130	(24–104)		
P	Haplic Phaeozem	Corn	None	1	>20	21		Richards et al. (1995)
	Loess subsoil under artificial sandy topsoil	Spring wheat	None	1	>30		(37–85)	Kuhlmann and Baumgärtel (1991)
	Silty loam	Corn	0 or 227 kg N ha^{-1}	1	26–80		(3–4)	Barber and Mackay (1986)
	Luvisol from loess	Spring wheat	n.s.	1	31–90		30	Fleige et al. (1981)
K	Silty loam	Corn	0 or 227 kg N ha^{-1}	1	26–80		(<3–35)	Barber and Mackay (1986)
	Haplic Luvisol	Spring wheat	n.s.	1	30		(<30–65)	Fleige et al. (1983)
	Luvisol from loess (average of 34 sites)	Spring wheat	n.s.	1	30		34 (7–70)	Kuhlmann (1990)
	Clayey loam	Green manure crops	57 mg N kg soil^{-1}; 23 mg P kg soil^{-1}	2	>25		(42–67)	Witter and Johansson (2001)

n.s.: not specified.

the total P uptake of wheat (Table 2). Based on diffusion measurements in the laboratory Fleige et al. (1981) stated that the subsoil covered 30% of spring wheat’s P nutrition. In contrast to these comparatively high values, Barber and Mackay (1986) based on the model developed by Claassen and Barber (1974) calculated a 3–4% P uptake from the subsoil (26–80 cm) by *Zea mays* L. on a silty loam soil with a low P concentration, a high buffering capacity and a low effective diffusion coefficient for P in the subsoil.

In a long-term trial on a calcareous loess soil, Garz et al. (2000) found strong evidence for a significant P acquisition by crops from 50 to 100 cm soil depth. Richards et al. (1995) estimated P delivery from the subsoil without P fertilisation of about 21 kg P ha^{-1} y^{1} in a long-term experiment with permanent maize cropping. Results from static long-term field trials showed that the decrease of total P contents in the topsoil was considerably smaller than the P uptake by the plants, a fact that can be explained by mobilisation of one part of the absorbed P from the subsoil (Wechsung and Pagel, 1993; Stumpe et al., 1994; Gransee and Merbach, 2000). As a consequence, Kuchenbuch and Buczko (2011) suggested reducing fertilisation recommendations oriented at the expected yield increase.

For potassium a number of long-term field studies suggest a substantial contribution of subsoil to total potassium uptake by plants (e.g. Blake et al., 1999; Srivastava et al., 2002). However, true tracer studies like for P or N are not available as the stable isotope of K (^{41}K) is very expensive and analysis of stable isotope ratios for potassium (^{39}K:^{41}K) is not yet a routine procedure due to the interference with ^{40}Ar^{1}H, ^{40}Ca^{1}H or ^{29}Si^{12}C during analysis (Becker et al., 2008). As an alternative to isotope dilution studies the K/Rb dilution method has been used by Kuhlmann (1990). Results from 34 field experiments on a Luvisol from loess in Northern Germany showed that the subsoil supplied on average 34% of the total K uptake by spring wheat (Table 2). The wide range from 9 to 70% could be explained by differences in exchangeable K in top and subsoils as well as the proportion of the root system exploring the subsoil (Kuhlmann, 1990). The role of root architecture was also demonstrated by Witter and Johansson (2001) using a similar approach as Kuhlmann (1990): the deep rooting forage crops *Cichorium intybus* L. and *Medicago sativa* L. acquired 56 and 67% of K from the subsoil as shown in a field study on clayey loam soil, whereas *Lolium perenne* L. displaying a high rooting density in the upper topsoil and a low rooting density in the subsoil acquired merely 42% subsoil K under the same experimental conditions.

Subsoil contribution to K uptake is likely to vary with climatic conditions. For spring wheat (*Triticum aestivum*) on a Haplic Luvisol Fleige et al. (1983) calculated a K delivery from the subsoil to range from <30% in a wet year to 65% in a dry year as a function of the soil water contents in the topsoils and subsoils. The fact that many arable soils in Europe show negative K field balances but no K deficiencies in the crop can be taken as another hint for the significance of nutrient delivery from the subsoil (Scherer et al., 2003; Öborn et al., 2005). An additional component of topsoil–subsoil interaction is the plant internal regulation of K uptake. It is well established that K influx into roots is regulated via recycling of K between shoot and root (Engels and Marschner, 1992; White, 1997). Thus, it can be expected that the extent of K depletion in the rhizosphere or the level to which K concentration in the soil solution decreases will depend on the K nutritional status of plants, which in turn is not a function of local K concentration but of total K availability in the whole root zone (Drew, 1975; Brouder and Cassman, 1994). Hence, it is possible that the magnitude of K release induced by plants in the subsoil is a function of K availability in the topsoil.

3.3. *Re-allocation and nutrient accumulation in the drilosphere*

Anecic earthworms use primary organic substances present at the soil surface, i.e. particularly crop residues as a food source and deposit plant material under decomposition as well as faeces and mucus inside their burrows, thereby transporting nutrient-rich material to the subsoil. Moreover, nutrients dissolved in water reach plant roots growing in pores or in the drilosphere via preferential flow. Consequently, areas around biopores could be preferred sites of nutrient acquisition in the subsoil. Watt et al. (2006) reported higher seepage and water flux in macroporous channels compared to adjacent bulk soil. Both anecic and endogeic earthworm species have an impact on soil water infiltration. In a soil column experiment Ernst et al. (2009) found accelerated water discharge at 55 cm depth in columns previously incubated

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with either *Allolobophora caliginosa* or *Lumbricus terrestris*, when compared with a control without earthworms. Particularly earthworm burrows with walls that are laterally less permeable to aqueous solutions than the bulk soil (Bastardie et al., 2005) can be expected to substantially enhance vertical water dynamics. So far, investigations on so-called preferential water flow, which may occur within macropores in pulses or thin films (Tofteng et al., 2002), mainly focused on possible alterations of soil properties rather than on its significance for plant growth, even when conducting measurements directly in the field (Villholth et al., 1998; Cey and Rudolph, 2009). Overall, it is plausible that preferential flow can lead to a particularly beneficial supply of water and nutrients to roots that enter these biopores on their way through the bulk soil.

Length and depth of biopores created by *L. terrestris* depend on soil temperature and moisture. In a microcosm study, burrow length of *L. terrestris* increased 6-fold when the temperature was increased from 5 °C to 20 °C at a soil matric potential of −11 kPa, whereas wetter soil (−5 kPa) at 20 °C resulted in burrow length of less than 1/3 of the drier soil (Perreault and Whalen, 2006). In addition, earthworm activity is influenced to a large extent by plant growth. Studies by Springett and Gray (1997) have shown the number of earthworm burrows significantly higher under *C. intybus* L. than under *L. perenne* L. or *M. sativa* L. According to Dreesmann (1994) crops affect the density of earthworm burrows by supplying variable amounts of nutrients to the worms in the form of undecomposed plant residues.

The drilosphere is a hot spot of soil biological activity (Table 3, Brown, 1995; Coleman et al., 2004). Compared with the bulk soil, soil compartments that are influenced by earthworm excreta are characterised by an overall higher number of microbes (e.g. Devliegher and Verstraete, 1997). In burrow walls of *L. terrestris* Tiunov and Scheu (1999) recorded increases of microbial biomass and basal respiration by factors of 2.4–4.8 and 3.7–9.1 respectively. A 1.5–2.5-fold increase of dehydrogenase activity (Jégou et al., 2001) indicates a generally higher biological activity in the pore wall. In addition, several authors have described an increase of certain functional groups in the drilosphere like ammonia oxidisers or microbes with the potential to express specific enzymes. For instance, Stehouwer et al. (1993) found the alkaline phosphatase activity in the drilosphere to be up to 6 times higher than in the bulk soil (Table 3). The higher microbial activity in the earthworm burrows is not only caused by higher C contents, but also by higher nutrient availability in the drilosphere compared with soil compartments not influenced by earthworm activities. Fresh earthworm burrows contain more bioavailable inorganic N in their walls than the bulk soil (Devliegher and Verstraete, 1997; Görres et al., 1997; Vinther et al., 1999), e.g. the NO_3^- contents was reported to be up to 1.6-fold higher (Parkin and Berry, 1999, Table 3). P and K contents (Graff, 1967; Pankhurst et al., 2002) as well as DOC contents (Vinther et al., 1999) are also elevated in the wall. In addition, the composition and availability of the P_o pool (Le Bayon and Binet, 2006) as well as nutrient-sorption properties of the drilosphere can differ from those in the bulk soil (Jensen et al., 2002). Even though most of the knowledge on drilosphere properties has been gathered in microcosm experiments the few studies undertaken on native subsoils indicate that the differences in chemical and microbiological properties between biopore wall and bulk soil are present at least down to a soil depth of 40–50 cm (Stehouwer et al., 1993) or 60–80 cm (Pankhurst et al., 2002).

Table 3
Relative drilosphere properties as compared to the bulk soil.

Parameter	Ratio 'drilosphere' to 'bulk soil'	Reference
C_{total}	1.8–3.5	Tiunov and Scheu (1999)
	2.6–4.4	Graff (1967)
C_{org}[a]	2.1–4.0	Pankhurst et al. (2002)
C_{hws}[b]	2–4	Stehouwer et al. (1993)
C_{min}[c]	3–4	Görres et al. (2001)
N_{total}	1.5–3.0	Pankhurst et al. (2002)
	1.3–2.2	Tiunov and Scheu (1999)
	2.3–4.3	Graff (1967)
NO_3^-	1.4–1.6	Parkin and Berry (1999)
NH_4^+	2	Devliegher and Verstraete (1997)
C/N	1.3–1.6	Tiunov and Scheu (1999)
	0.8–1.6	Graff (1967)
P_{total}	1.6–2.4	Graff (1967)
P (lactate extractable)	2.8–6.0	Graff (1967)
K (HCO_3^- extractable)	1.0–1.2	Pankhurst et al. (2002)
Ca, Cu, Fe, Mn	Significantly higher	Pankhurst et al. (2002)
Basal respiration	3.7–9.1	Tiunov and Scheu (1999)
Microbial biomass	2.4–4.8	Tiunov and Scheu (1999)
Dehydrogenase activity	1.5–2.5	Jégou et al. (2001)
Alkaline phosphatase activity	2.5–6.0	Stehouwer et al. (1993)
Bulk density	1.1	Schrader et al. (2007)
Moisture (Θ)	1.3	Görres et al. (2001)
Specific pore volume	0.8–0.9	Görres et al. (2001)
Median pore neck diameter	0.5–0.7	Görres et al. (2001)

[a] Organic carbon.
[b] Hot-water soluble carbon.
[c] Carbon mineralization rate (μg CO_2-C g^{-1} d^{-1}).

Apart from the drilosphere, in arable subsoils organic matter can also be enriched in tongue-formed zones which contribute to the spatially heterogeneous distribution of nutrients (Chabbi et al., 2009). These authors attribute the presence of such 'tongues' to fresh C input by preferential flow and/or roots. The re-allocation of nutrients and organic matter to the subsoil therewith contributes to the formation of a heterogeneous environment in deep soil layers.

3.4. *Quantification of nutrient acquisition from the subsoil by mathematical modelling*

3.4.1. *Process based models*

Quantification of nutrient acquisition from the subsoil will improve the estimation of nutrient balances for different crops and cropping systems, and the environment. Importantly, the complexity of processes involved (see conceptual model above and Fig. 2) requires a systems approach. Such approach emphasises the integration of these processes considering also above ground growth processes and their responses to climatic conditions and management, and accounting for important dynamic feedback loops between processes.

Process based models (PBMs) are based on systems thinking and integrating information from different processes into a coherent mathematical model. PBMs simulate physiological processes and describe metabolism and crop growth in terms of mass variables per unit area of land (Vos et al., 2010). Most of these models consider the uptake of water and N along the vertical soil profile down to the maximum rooting depth, i.e. they consider nutrient uptake throughout the rootable soil depth. In the last decades, substantial progress has been made in the modelling of growth and development processes of crops with regard to climate factors, soil properties, water and nutrient supply (Donatelli et al., 2002; van Ittersum and Donatelli, 2003; Shepherd et al., 2011). Prominent examples are CropSyst (Stöckle et al., 2003), DSSAT (Jones et al., 2003), APSIM (Keating et al., 2003), STICS (Brisson et al., 2003) and the different models of the Wageningen school (van Ittersum et al., 2003). However, PBMs exhibit major shortcomings with respect to nutrient uptake from the subsoil: (i) most of these models only consider water stress and N, ignoring other nutrients such as P and K or micronutrients limiting crop growth and yield, (ii) the structural and chemical differences in horizontal direction (i.e. within the same soil layer) are neglected, and (iii) several processes mentioned above (Sections 3.1–3.3) such as biopore formation or nutrient re-allocation and accumulation in the drilosphere are often ignored or treated in a strongly simplified way and their relative importance for the overall systems behaviour is not well understood. Several attempts have been made to overcome these limitations.

Besides N only a few PBMs additionally consider soil phosphorous dynamics and uptake by crops, e.g. CENTURY (Parton et al., 1987), APSIM and DAYCENT (Parton et al., 1998) and even fewer models consider K in addition to water, C, N and P, e.g. EPIC (Williams et al., 1984) with the upgrade for K (Barros, 2004) and FIELD (Tittonell et al., 2007). However, the validity of these approaches for the specific characteristics and processes of the subsoil remains untested. Kuka et al. (2007) proposed a general approach to take into account the effect of pore size classes and the carbon pools associated to these classes on soil organic matter dynamics which could be extended to simulate the effect on N turnover. Few examples are known in which root growth has been modelled taking biopores into account (Jakobsen and Dexter, 1988; Stirzaker et al., 1996), but these have not yet been incorporated into system models. Jakobsen and Dexter (1988) also reported on simulating the effect of biopore density in the subsoil on crop water uptake and transpiration. So far, the effect of biopore density on subsoil nutrient acquisition has not been taken into account.

Nutrient translocation is represented by most PBMs following the allocation of C, often based on development-dependent allocation fractions to plant organs combined with an organ-specific optimal nutrient concentration (e.g. van Ittersum et al., 2003). More advanced approaches consider sink–source interaction and metabolic relationships determining nutrient allocation between the plant shoot and other organs (Yin and van Laar, 2005). Some PBMs explicitly consider deposition of residues to the topsoil, e.g. SUNDIAL (Bradbury et al., 1993). However, studies to test the capability of PBMs to simulate nutrient accumulation in the topsoil as a consequence of litter fall and belowground remobilisation of nutrients are lacking.

The effect of earthworms on biogeochemical cycles (e.g. C and N cycles) has been included in models by itemising a specific ‘earthworm-pool’ that interacts with fresh organic matter, soil organic matter and microbial biomass (Huang et al., 2010). This pool has a similar function as the ‘microorganisms-pool’ that is included in carbon and nitrogen cycle models. The redistribution or reallocation of substances in the soil by earthworm or soil fauna, i.e. bioturbation, has been described in models as an advective-diffusive process whereby specific parameters for the biological advective speed and biological diffusion have been defined as a function of soil depth to account for variations in biological activity with depth. These models were used to simulate the transport of less mobile substances in the soil, e.g. radionucleides (Bunzl, 2002) and arsenic (Covey et al., 2010). To assess the impact of earthworm burrows on soil functions that are closely related to soil structures, models that generate realistic earthworm burrows in virtual soil blocks have been developed (Bastardie et al., 2002; Blanchart et al., 2009). By simulating water flow and solute transport using detailed three dimensional flow and transport models in such generated virtual soil blocks with earthworm burrows, the effect of burrows on soil properties such as hydraulic conductivity (Bastardie et al., 2002) and preferential transport was evaluated (Vogel et al., 2006; Sander and Gerke, 2009).

3.4.2. Functional–structural plant models

The impact of biopores, subsoil heterogeneity, and lateral variations of nutrient availability cannot be considered explicitly but must be parameterised implicitly in PBMs. This implies that these models could be used to describe nutrient and water uptake from heterogeneous subsoils when properly parameterised but cannot be used to predict uptake as a function of structural parameters that characterise subsoil heterogeneity. Since these models do not consider the mechanisms of the uptake processes in detail, also uptake from soil profiles with vertical gradients in water and nutrient contents needs to be parameterised.

Functional–Structural Plant Models (FSPMs) (Godin and Sinoquet, 2005) were developed to account explicitly for plant structural features in the prediction of crop growth. Such models are made for 3-D plant scale modelling and they predict root growth and water acquisition based on 3-D distribution of resources and constraints (light, water, solute nutrients, assimilates), whereas the uptake of nutrients except N has been neglected so far. As a consequence, these models provide a link between structural features of root and soil architectures and nutrient and water uptake from heterogeneous subsoils. As compared to PBMs, FSPMs need more physical parameters, a spatially explicit description of soil and root structures and require much more detailed data. They are made for 3-D plant scale modelling. FSPMs typically allow considering the impact of 3-D variable soil properties for root growth, solute and water uptake. Mainly models for the aerial parts of the plant have been developed, whereas FSPMs for the belowground part of the plant accounting for interactions with the soil and with nutrients are scarce (Draye et al., 2010; Javaux et al., 2010). Somma et al. (1998), Dunbabin et al. (2002) and Pagès et al. (2004) present root architecture models that predict root development as a function of soil environmental conditions. Dunbabin et al. (2004) demonstrate that the plasticity of root development to spatially varying soil environmental conditions, e.g. spatially variable N concentrations, is crucial to predict the functionality of a root system.

FSPMs consider processes at the scale of an individual root and models for transport of nutrients from the bulk soil towards the soil–root interface and for nutrient uptake as function of root surface concentrations have been developed (Barber, 1995; Nye and Tinker, 1977). At this scale, also rhizosphere processes leading to different conditions at the root surface than in the bulk soil can be implemented in these models. For instance, some dynamic models for rhizodeposition were suggested and experimentally parameterised for *Lolium* spp. (Kuzyakov et al., 1999; Kuzyakov and Domanski, 2002). The effect of exudates on desorption of phosphate (Szegedi et al., 2008; Dunbabin et al., 2006), the effect of root hairs on nutrient uptake (Leitner et al., 2010) and the impact of mycorrhizal fungi on phosphorus uptake (Schnepf et al., 2008) have been implemented in root scale models. In order to include rhizosphere processes in models that describe the entire root system of a plant, local-scale process models, which may be approximately but computationally efficiently described by analytical solutions of the flow and transport equations (Roose and Kirk, 2009; Schröder et al., 2009) were coupled with root system scale models. At the root system scale, flow and transport processes in the root system, at the soil–root surface and in the soil have to be coupled. The main reasons are probably the difficulty of observing and understanding the functioning of plant roots and the interactions between root growth and soil. Several models explicitly simulate 3-D root growth, but they typically do not consider the effect of limitation in assimilates and nutrients on root growth and they consider only 1-D vertical distributions of nutrients and water contents in the soil profile (e.g. Pagès et al., 2004). Recently Doussan et al. (2006) and Javaux et al. (2008) have built a model which solves the water flow equations in the soil and in the root xylem network and allows calculation of the uptake flux distribution between soil and root. Three dimensional solute transport in the heterogeneous soil and simple uptake processes are also included. Such an integrated soil–root model offers the opportunity to link root development plasticity, dynamic soil environmental conditions, root uptake processes, and flow and transport processes in a heterogeneous soil. Such integration is essential to predict uptake from the subsoil as a function of environmental conditions, subsoil structure and nutrient distribution in the subsoil.

4. New approaches for measuring and quantifying nutrient acquisition from the subsoil

In many cases, the knowledge gaps regarding nutrient acquisition from the subsoil are due to a lack of adequate and simple methods for subsoil investigation. Whenever the native physical state of the subsoil or root growth has to be taken into account, usually destructive soil sampling is required which is laborious and time-consuming. However, recent technological advances will allow more detailed and more feasible views into subsoil processes (Table 4). 'Non-invasive' or minimum-invasive methods such as advanced scanning approaches now become a promising alternative to destructive methods for assessing soil structure and root growth in the subsoil, but so far they are hardly available for field studies. When these methods are used in microcosm studies, soil monoliths must be obtained with suitable excavation devices avoiding soil compression or rupture. New technologies which cut the outline of the soil monolith with a rotary cutting system allow the excavation of such undisturbed monoliths (Meissner et al., 2007, 2010).

Subsoil-structure development through plant growth and earthworm activity with time can be studied on various scales (from pedon to the rhizosphere) by X-ray computed microtomography. In combination with quantitative morphological image analysis metrical data of the pore networks such as pore connectivity, tortuosity and pore wall surface area can be derived (Peth, 2010) and utilised by mechanistic biogeochemical and transport models. Optical monitoring of root growth via infrared image segmentation (Nagel et al., 2009), X-ray computed microtomography (Carminati et al., 2009), nuclear magnetic resonance (NMR) imaging (van As and van Dusschoten, 1997) and neutron radiography (Carminati et al., 2010; Esser et al., 2010) can improve the dynamic understanding of the effect of abiotic factors on root growth, root–shoot exchange processes and the establishment of root system architecture in artificial soil systems or soil cores taken from the subsoil. Promising for the non-invasive monitoring of root systems at the field scale are electrical geophysical methods. Electrical resistivity tomography (ERT), in which the subsurface electrical conduction properties and their spatial distribution are measured by injecting electric current and measuring resultant voltages on an array of surface electrodes can provide spatially resolved information on water content changes and thus root water uptake (Michot et al., 2003; al Hagrey, 2007; Srayeddin and Doussan, 2009). Furthermore, the electrical polarisation properties can be measured, which is done in electrical impedance spectroscopy (EIS) over a range of measurement frequencies. Laboratory measurements have shown that the sensed polarisation signal is directly related to parameters such as root mass and length (Ozier-Lafontaine and Bajazet, 2005; Repo et al., 2005), making EIS an appealing approach for root system characterisation and monitoring at the field scale. A new approach for assessing root growth in biopores is the use of flexible endoscopes directly introduced into the pore lumen. Kautz and Köpke (2010) used this technique to display root morphology and position inside of biopores. Endoscopy might also be of particular relevance for quantifying the contact areas between root and pore wall.

Characterisation of microbial community structure and function in soil based on directly extracted nucleic acids from soil and subsequent sequencing became possible quite recently (Daniel, 2005). Therefore today we can describe abundance, diversity and activity patterns of selected functional groups of bacteria, fungi and archaea (Ollivier et al., 2011). It has even been shown that this approach allows the reconstruction of whole microbial genomes from soil (Vogel et al., 2009). Together with the use of stable isotopes this new type of information allows us to identify new biotic and abiotic drivers for selected functional traits to predict potential and actual activity patterns as well as to answer questions related to functional redundancy and resilience in soil.

Micro suction cups enable us to study the dynamics of soil solution chemical composition at high spatial resolution, i.e. along roots and with increasing distance from roots in situ in a non-invasive way (Dieffenbach and Matzner, 2000; Vetterlein and Jahn, 2004; Dessureault-Rompré et al., 2007). The technique can be applied in microcosm experiments (compartment system or root box experiments) as well as under field conditions (along root windows). The limitations for this technique are related to detection limits of chemical analyses and sample volume required for this step.

Studying nutrient uptake from undisturbed subsoils often uses stable isotope methods which are, in the case of P, not available. ^{32}P and ^{33}P may not be investigated in field studies. Hence, ^{18}O labelled phosphate is a promising tool for investigation of P in the environment which is currently under evaluation (Tamburini et al., 2010; Angert et al., 2012). However, methodological constraints with respect to biological processes involved have to be considered for nutrient uptake studies (Larsen et al., 1989).

The approaches discussed here have not only the potential to improve our ecological understanding about subsoils, but will also help to improve process orientated models on nutrient acquisition from subsoils.

4.1. New modelling approaches: linking crop scale with root system scale models

To date, crop scale models and root system scale models have only been developed separately but never been linked. With particular respect to the various spatial scales involved in processes of nutrient acquisition from the subsoil (Fig. 1, Table 4), integration of the crop scale models that are used to predict field-scale crop growth, nutrient and water uptake and smaller scale models would be needed. Assuming that processes on the root system scale must be taken into account to adequately represent nutrient acquisition from the subsoil, a promising avenue to advance modelling of nutrient acquisition and uptake is the linking between PBMs and FSMPs. Three dimensional small scale functional structural root-system models are computationally expensive which prohibits their application at the crop and field scale. Thus, a link between these smaller scale models and the field scale PBMs that are used to predict crop growth, nutrient and water uptake is required. Simulations with root-system scale models could be used to derive suitable concepts and effective parameters for describing water and nutrient uptake from heterogeneous subsoils in crop and field scale PBMs. Simulation experiments with root-system scale models for a range of typical soil structures and properties could provide datasets against which crop scale models could be parameterised so that relationships between crop scale model parameters and soil structure parameters could be inferred. Real experimental data constitute the basis for all model simulations. But simulation

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Table 4
New approaches for understanding processes of nutrient acquisition from the subsoil (● applicable; ○ not yet demonstrated; – not applicable).

Method	Parameters	Spatial scale taken into account	Resolution	Applicability		References
				Field studies	Microcosm studies	
X-ray µCT	Biopore network characteristics (connectivity, tortuosity, pore wall surface area, diameter) and root growth dynamics in soil in situ	3-D systems; Pore to pedon scale	(1–250 µm depending on sample diameter)	–	●	Carminati et al. (2009), Peth (2010)
Nuclear magnetic resonance (NMR) imaging	Measurement of root growth dynamics in soil in situ	3-D systems; 10 cm	200 µm	–	●	Nagel et al. (2009)
Neutron radiography	Root structure and element composition in situ	2-D 15 × 15 cm, layer thickness limited to several mm	<100 µm	–	●	Carminati et al. (2010), Esser et al. (2010)
pH monitoring	Exchange of protons between root and rhizosphere	2-D systems, several cm	2 mm	–	●	Blossfeld and Gansert (2007)
Near-Infrared optical imaging	Root growth dynamics in cellular resolution	10 mm	10 µm	–	●	Nagel et al. (2009)
Electrical resistivity tomography (ERT)	Changes in water content due to root water uptake; soil structure	Horizontal: dm–100 m, vertical: dm–10 m, depending on electrode layout	cm–m, depending on electrode spacing	●	●	Michot et al. (2003), al Hagrey (2007), Petersen and al Hagrey (2009), Srayeddin and Doussan (2009)
Electrical impedance spectroscopy (EIS)	Root mass, root length	In principle like for ERT; studies so far only dm	In principle like for ERT; studies so far only dm	○	●	Ozier-Lafontaine and Bajazet (2005), Repo et al. (2005)
In situ-endoscopy	Contact between roots and biopore wall; presence of biopore coatings and macropore root soil	Coarse biopores (>5 mm diam.)	<100 µm	●	●	Kautz and Köpke (2010)
Next generation sequencing of extracted DNA and RNA from soil	Barcoding of microbial communities to measure diversity pattern in soil; analysis of metagenomes from soil to assess regulatory networks; reconstruction of microbial foodwebs	mm–cm	100 mg–10 g of soil	●	●	Vogel et al. (2009), Gubry-Rangin et al. (2011)
Stable isotope probing	Analysis of microbes using specific substrates	mm–cm	100 mg–10 g of soil	●	●	Prosser et al. (2006)
Quantitative PCR of extracted DNA and RNA from soil	Cultivation independent quantification of specific microbes carrying specific functional traits	mm–cm	100 mg–10 g of soil	●	●	Sharma et al. (2007)
Combining micro suction cup techniques with X-ray diffraction analysis	In situ measurement of soil solution composition with high temporal and spatial resolution is combined with identification and quantification of soil minerals in the rhizosphere	Gradients extending from the rhizosphere (mm to cm)	About 6 mm for soil solution, 1 mm for X-ray diffraction on sliced soil samples	–	●	Vetterlein and Jahn (2004), Vetterlein et al. (in preparation)
Stable isotopic dilution: Labelling of the surface soil with $^{18}O\text{-}PO_4$	PO_4 turnover in soil, PO_4 uptake from subsoil	≤¼ m^2	To be evaluated	●	●	Larsen et al. (1989), Tamburini et al. (2010), Angert et al. (2012)

experiments provide a tool to explore a range of conditions systematically and separate the effect of individual processes.

Since root system models do not generally consider the above ground part of a plant, there is no feedback between nutrient and water uptake, shoot growth and carbon assimilation, and root growth and development. Thus, the coupling of crop growth and crop development that is simulated by crop scale PBMs as a function of the total nutrient and water uptake should therefore provide a feedback into root system scale models and *vice versa*. In a similar vein, models that simulate the activity of soil fauna as a function of soil properties and addition of fresh organic matter, the effect of soil fauna on biogeochemical cycles, and the effect of soil fauna on reallocation of nutrients by bioturbation to the subsoil should be integrated in crop scale models. Models that simulate soil faunal activity may also be used to provide smaller scale information about the distribution of biopores, nutrients, and soil properties in the vicinity of biopores, which is crucial input for models that simulate root growth and nutrient uptake at the root scale.

5. Agronomic strategies for enhanced accessibility to subsoil nutrients

For field crops, spatial access to subsoil nutrients depends on the development of a dense and extensive root system. Compacted soil layers may impede root penetration and thus limit the exploration of subsoil nutrients. Among others, Ehlers et al. (1983) have shown that in untilled cropping systems, severe soil compactions caused by machinery traffic (so called 'traffic pans') are avoided and root growth into deeper soil layers is facilitated.

However, in temperate climates the establishment of no-till systems to low-input production systems such as organic farming (where pronounced interest in subsoil contribution to nutrient uptake is given) so far has been hindered by retarded nutrient mobilisation and weed infestation (Köpke, 2008; Köpke and Schulte, 2008). In cropping systems using ploughing, 'subsoiling' (i.e. deep mechanical loosening of the soil below the routine ploughing depth) as well as the promotion of biopore formation are two general strategies for improving subsoil rootability. In addition, we assume that agricultural management with potential for increasing organic matter contents in the subsoil (e.g. frequent application of manure) or maintaining high soil water contents in the subsoil (e.g. avoidance of highly water demanding crops in the rotation) can facilitate accessibility to subsoil nutrients. However, such potential effects have not yet been quantified.

5.1. Deep mechanical soil loosening (subsoiling)

On soils where a compacted traffic pan hinders crop roots to grow into the subsoil, amelioration by deep mechanical loosening can lead to enhanced root growth, N uptake and shoot growth, as shown for winter wheat on a light-textured sandy loam by Barraclough and Weir (1988). Recently, Himmelbauer et al. (2010) determined root growth in the subsoil and shoot biomass production of maize higher after melioration consisting of deep loosening and drainage. However, a potential limitation of subsoiling – apart from the comparatively high demand for energy and the related costs – is the risk of re-compaction due to subsequent tillage events or trafficking the soil. On a loamy Entic Haplustoll Botta et al. (2006) found the effects of subsoiling on penetration resistance to be eliminated during the following growing season. Sojka et al. (1997) reported positive effects of subsoil loosening on emergence and yield of oats on a Typic Haplaquoll only when the soil was not tilled afterwards. Adverse effects of deep mechanical loosening have been reported also: Munkholm et al. (2005) found a decrease in root growth and grain yield of winter wheat grown on a sandy loam in treatments loosened to 35 cm soil depth with a subsoiler and re-compacted by traffic and mouldboard ploughing when compared with a conventional tillage system without subsoil loosening. These authors attribute this effect to a potential destruction of continuous biopores in the mechanically loosened subsoil and recommend deep mechanical loosening for severely compacted subsoils only. Generally, the chance of success seems to vary considerably with site and weather conditions. Several studies revealed positive effects of subsoiling on crop yield predominantly or exclusively in dry years (Marks and Soane, 1987; Olesen and Munkholm, 2007). Batey (2009) reviewed various experiments on the effects of subsoiling on crop growth with variable results and concludes that yield responses depended largely on the extent of moisture stress experienced by the crop.

5.2. Promotion of biopore formation

Rooting and earthworm activity contribute to subsoil biopore formation in arable soils. In various microcosm studies with homogenised and recompacted soil, deep-burrowing (anecic) earthworms have been reported to create biopores over time periods between a few days (Joschko et al., 1989) up to 6 months (Francis and Fraser, 1998). To date, possibilities to remedy compacted soils by earthworms were intensively investigated (Langmaack et al., 2002). However, recent studies have shown that earthworms generate more biopores in non-compacted soil zones (Capowiez et al., 2009). The preference for non-compacted zones also leads to the assumption that earthworms at least partially colonise existing biopores that were created by roots. Pre-existing pores can be widened by earthworms and stabilised by lining the pore wall with mucus and faeces. Various interactions between earthworm activity and plant growth may occur. Ingestion of roots was reported for various species but merely as a minor component of the ingested material (Gunn and Cherrett, 1993; Brown et al., 2004). In contrast, the presence of earthworms was found to stimulate root growth and total shoot biomass of various crops such as *Poa annua* (Scheu et al., 1999; Laossi et al., 2009).

When roots grow through the bulk soil, they cylindrically compress the soil around them (Dexter, 2004). Due to the compression of soil adjacent to the root and the release of mucilage from the root tip, the created void remains stable after root death. Wiermann et al. (2000) amongst others argued that the increased strength of these voids results from the equilibration with the vertical (major) stresses which is furthermore increased by the parallel alignment of the adjacent soil particles during root growth. If we also take into consideration the effect of a more intense drying in the vicinity of the root surface we also can assume higher soil strength of the rhizosphere region compared with the bulk soil which is furthermore enhanced by the increased hydrophobisation of the surfaces. Decaying roots leave a continuous network of vertically oriented round shaped macropores that can be used by subsequent crops (Volkmar, 1996). Generally, dicotyledons are assumed to create more stable biopores than monocots (Materechera et al., 1993). This can be explained by the higher proportion of thicker roots present in dicots, which are more capable of penetrating even compact soil layers than thinner roots (Materechera et al., 1992) and by the enhanced stability of biopores with increasing diameter (Logsdon and Linden, 1992). Perennial and taproot cropping is considered to be more effective in enhancing biopore density in the subsoil than cropping systems with annual crops only because of the apparent ability of perennial root systems to create a more stable, continuous pore network (Benjamin et al., 2007). In a comparison of six different cropping systems the presence of grass-clover leys increased earthworm density, biomass and burrow density (Riley et al., 2008). Root system turnover rates of crop species are highly variable and primarily a function of water and nutrient supply, temperature, root diameter and the grazing/cutting regime (Lauenroth and Gill, 2003). However, a mean turnover rate for root systems in temperate grassland of half a year (Gill and Jackson, 2000) indicates that perennial crops continue to modify soil structure by persistent root growth also in the 2nd and 3rd year of cultivation. In compacted soils, perennial fodder crops with taproot systems were successfully grown to increase the macroporosity (Lesturgez et al., 2004). McCallum et al. (2004) found that the number of larger biopores (diameter > 2 mm) had increased after 4 years of continuous lucerne cropping, and recorded these biopores remaining stable for at least two annual crops grown after lucerne. Apart from effects on soil structure and soil nutrients, pore systems formed by the roots of perennial fodder crops may also have a direct influence on root growth of subsequent crops. Kirkegaard et al. (2008) reported the longevity and close association of residues of previous root systems and their associated organisms with root growth of current crops.

Likewise, growing of perennial fodder crops may indirectly affect earthworms by temporarily omitting tillage (soil rest) and directly by providing a suitable food source in form of shoot and root residues. Tillage is known to reduce earthworm populations either by direct mechanical disturbance or by provoking negative impacts on soil climate and soil structure (Edwards and Bohlen, 1996). Inversion tillage exposes earthworms to predation and desiccation and is especially harmful to (anecic) species (review by Holland, 2004). Hence, reducing tillage intensity or omitting tillage occasionally may increase earthworm populations (Emmerling, 2001; Wuest, 2001; Curry et al., 2002; Kautz et al., 2011) and even result in higher macropore densities in the subsoil, which was demonstrated with the classic work of Ehlers (1975). Apart from the tillage frequency, modifying the crop sequence may affect earthworm populations. Schmidt et al. (2003) found the earthworm abundances under wheat undersown with clover to be twice as high as compared with a pure wheat stand. Hulugalle et al. (1999) reported that lucerne can increase earthworm activity, numbers of earthworm burrows and air filled porosity. In comparison with a crop rotation with annual inversion tillage Kautz et al. (2010) observed that perennial forage crops caused higher soil C and N contents, higher biomass and abundance of anecic earthworms and higher densities of medium and coarse biopores in 35 cm soil depth. Also in this case it is assumed, that under perennial fodder crops root growth and earthworm activity interact in biopore formation. It is probable that these ‘new’ biopores in the subsoil promote nutrient acquisition. The quantification of biopore effects on nutrient acquisition from the subsoil is subject to ongoing research activities.

6. Conclusions

More than two-thirds of soil nutrients can be found in subsoils, therewith potentially contributing to plant growth. However, the accessibility of these nutrients for plant growth is limited due to higher compaction, lower oxygen content and microbial activity, along with lower root length density and lower degree of mycorrhizal infection. Due to the relevance of long-term processes prevailing under native, i.e. structured subsoil conditions, precise quantification of the subsoil impact on plant nutrition is delicate from short-term studies or microcosm experiments with disturbed soil. Thus, our current knowledge on subsoil processes must be considered to be rather vague. The data currently available indicates that the extent to which subsoils contribute to plant nutrition may vary greatly from <10% of total plant uptake to >70% for certain soil nutrients. These huge variations are partly induced by environmental conditions: in particular, a dryer topsoil forces the plants to utilise water and nutrients from deeper subsoil horizons. Since with the on-going global climate change it is expected that summer drought will more commonly affect regions under agricultural use (e.g. in Central Europe), exploration of subsoil water and nutrient resources could be of increased future relevance. Long-term agricultural field experiments tend to indicate that lack of topsoil fertilisation might promote the acquisition of subsoil’s nutrients in the long-term. Thus the potential of subsoil for nutrient acquisition from the subsoil can be expected to be particularly high in low-input farming systems such as organic agriculture.

Accurate estimates of processes involved in nutrient acquisition from the subsoils such as root growth and its interactions with soil structure are difficult to obtain, because most of the available research ignores the subsoil. Novel imaging techniques like X-ray μCT, NMR, EIS, and endoscopy, in the best case in combination with stable isotope tracing techniques, may offer an experimental solution to this research gap. Nevertheless, the complete quantitative understanding of the role of subsoils for nutrient uptake requires integration of processes on various spatial and time scales. This can be obtained by modelling, especially when crop scale models can be linked with root system scale models, which has not been done so far. Nevertheless, there is clear evidence that the portions of nutrients acquired from the subsoil depend on the preceding crops, soil animals and climate. Biopore formation by earthworms and old deep root systems fertilise the subsoils with nutrients from the topsoil and increase the accessibility of suboils for current root growth. Thus, biopores in the subsoil must be understood as hot spots for nutrient acquisition in an environment which is otherwise adverse for root activity. The promotion of biopores appears to be more sustainable than mechanical subsoiling and provides potential for improving the efficacy of nutrient cycling in arable soils, though precise quantification of biopore contribution to nutrient acquisition from the subsoil is still missing.

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