Trends in Plant Science

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Review

Digging Deeper for Agricultural Resources, the Value of Deep Rooting

Kristian Thorup-Kristensen,[1,*] Niels Halberg,[2] Mette Nicolaisen,[1] Jørgen Eivind Olesen,[3] Timothy E. Crews,[4] Philippe Hinsinger,[5] John Kirkegaard,[6] Alain Pierret,[7,8] and Dorte Bodin Dresbøll[1]

In the quest for sustainable intensification of crop production, we discuss the option of extending the root depth of crops to increase the volume of soil exploited by their root systems. We discuss the evidence that deeper rooting can be obtained by appropriate choice of crop species, by plant breeding, or crop management and its potential contributions to production and sustainable development goals. Many studies highlight the potentials of deeper rooting, but we evaluate its contributions to sustainable intensification of crop production, the causes of the limited research into deep rooting of crops, and the research priorities to fill the knowledge gaps.

Highlights

Recent studies have documented highly significant differences among current and potential crops, as well as genotypic differences, in the ability for deep rooting.

Results have shown significant effects of deep roots on deep soil water and nutrient uptake.

Technological improvements of nondestructive methods, such as rhizotron and image analysis based root observations, soil water sensors, and isotope tracers for uptake studies, allow combined and dynamic studies of root development and function.

The quest for sustainable intensification of crop production promotes the interest in understanding and exploiting the potential contribution by deeper soil layers. Deep layers may contribute to resource supply for crop growth, reducing losses to the environment and deep C sequestration to mitigate climate change.

The Quest for Sustainable Intensification

The triple challenge to increase food and biomass production, adapt to and mitigate climate change, and reduce the negative impacts on natural capital and environment has been termed the perfect storm [1]. There are limited options to increase the area under intensive farming, and converting new land to agriculture would be at the expense of nature and biodiversity already under pressure [2]. Agricultural activities currently cause nutrient loading to aquatic and terrestrial ecosystems, often exceeding ecologically tolerable levels, and also contribute to land use change, deforestation, freshwater depletion, and climate change [3]. In addition, climate warming and greater weather variability increasingly challenge agricultural production systems, prompting calls for radical changes to sustain food production [4,5].

A neglected topic in the quest for sustainable intensification is better exploitation of deep soil profiles using novel crops, genotypes, and cropping systems with substantially greater effective rooting depth. Rooting depths beyond those of commonly grown crops can increase the resource base available for crop production and minimize nutrient losses to the environment, without using more land or external inputs. We explore the prospects to extend the '3rd dimension' of agricultural land by considering our current understanding of deeper rooting as a tool to contribute to sustainable food production, some of the promising strategies, and a research agenda to put this idea into practice (Box 1).

We consider the potential to develop effective deeper rooting in cropping systems and the potential impacts on crop production and sustainability. Specifically, we address the following questions: (i) Under what circumstances can crop roots grow deeper? (ii) What resources may they acquire from the previously unexploited deeper soil layers? (iii) How could a deeper-rooted agriculture affect soil fertility, soil ecology, and soil C storage?

Is There a Biological Potential for Deeper Rooting?

Deep rooting varies substantially between different climates, ecosystems, soil conditions (Box 2), and plant species or genotypes. Most plants in natural habitats grow considerably deeper roots than agricultural crops [6]. Trees and shrubs have the deepest average rooting depths (7.0 ± 1.2 m and

[1]Department of Plant and Environmental Sciences, University of Copenhagen, Thorvaldsensvej 40, 1871 Frederiksberg C, Denmark
[2]DCA - Danish Centre for Food and Agriculture, Aarhus University, Blichers Allé 20, 8830 Tjele, Denmark
[3]Department of Agroecology, Aarhus Universitet, Blichers Allé 20, 8830 Tjele, Denmark
[4]The Land Institute, 2440E Water Well Rd. Salina, KS 67401, USA
[5]Eco&Sols, University of Montpellier, CIRAD, INRAE, IRD, Montpellier SupAgro, Montpellier, France
[6]CSIRO Agriculture and Food, GPO Box 1700, Canberra, ACT, 2601, Australia
[7]Institut d'Écologie et des Sciences de l'Environnement de Paris (iEES-Paris), Sorbonne Université, CNRS, INRAE, IRD, Université de Paris, Université Paris Est Creteil, Paris, France

[8]Department of Agricultural Land Management (DALaM), Ministry of Agriculture and Forestry, Vientiane, Lao PDR

*Correspondence:
ktk@plen.ku.dk (K. Thorup-Kristensen).

Box 1. Challenging One Last Frontier: Understanding and Improving Deep Rooting

Current agricultural systems do not utilize subsoils efficiently. In an ongoing project, DeepFrontier, the potential use of deep-rooted crops to improve environmental performance and resilience of food production is studied. Our knowledge of deep rooting of crops is limited, mostly because deep root studies are demanding and there is a lack of methods making larger scale studies feasible. In the DeepFrontier project we work on all the aspects of this gap in knowledge. We study deep rooting of agricultural crops (in this project defined as between 1 and 5 m depth) and how to achieve it. We study the uptake functions of deep roots and their effects on subsoil microbial communities and C storage, and we work to develop methodologies for deep root studies.

Many deep root studies are limited to few observations in time and space, constraining comparative studies or dynamic studies of growth and function. In the DeepFrontier project we have developed new facilities aimed at solving some of these issues. One facility is the ‘Root towers’, comprising 24 growth containers, each 4 m high and with a surface area of 0.3 × 1.2 m. Each container enables root observation through transparent Perspex windows over most of the 1.2 × 4 m surface, and direct access to the soil, to add tracers or collect soil or root samples. Time-domain reflectometry (TDR) soil water sensors are installed at four depths within each chamber. Thus, the facility allows simultaneous studies of root system development and activity at all depths down to 4 m depth in replicated treatments (see Technology of the Month).

In addition, we have built a field facility, the ‘Deep Root Lab’, also with improved access to observe roots and study their function under realistic field conditions. We have established 24 plots (10 × 19.5 m) each equipped with six minirhizotrons to 5 m depth for root observation and six access tubes for studies of root activity. The access tubes are steel tubes with openings at different intervals to a maximum depth of 4.4 m. Within the access tubes, ingrowth cores with soil samples can be inserted to apply tracers for studies of root uptake at various soil depths, and root length and biomass can be determined when ingrowth cores are retracted. Finally, the facility is equipped with TDR sensors in three depths down to 2 m depth.

5.1 ± 0.8 m, respectively) with some tropical trees growing roots to extreme depths of 20–50 m or more [6]. Compared with this, temperate grassland plants and crops are shallow rooted with average rooting depths of 2.6 ± 0.1 m and 2.1 ± 0.2 m, respectively [6]. However, as pointed out by Schenk and Jackson [7] and further discussed by Pierret *et al*. [8], the available data defining maximum rooting depth of different crops is often limited by the depth of measurement rather than the actual maximum rooting depth.

Deep root growth and associated water and nutrient acquisition vary strongly among crops, with reported rooting depths varying from less than 0.3 m to more than 3 m among common agricultural crops [9–11]. It is well known that some crop or pasture plants, such as lucerne [12], sugar cane [13], sugar beet [14,15], sunflower [11,16], and some cruciferous crops [9,10] have the potential to grow roots to well below 2 m depth.

Box 2. Soil Constraints to Deeper Rooting

There is a strong biological variation in the potential for deep rooting among crops, but in practice rooting is also determined by soil properties. Deep soil layers are inherently less hospitable for root development, due to higher compaction and much less organic matter than in the topsoil. In many regions the porous soil layers overlay rock at some depth, allowing limited or no root penetration, though substantial areas with highly weathered Ferralsols and Arenosols are found in the tropics. Even where soil physics do allow root penetration, other factors may limit it. One common factor is water, where the soil may be too dry for root growth and function or it may be waterlogged and anaerobic, thereby limiting root development. Restrictive chemical conditions such as acidic subsoils or high salt concentrations are also found in some areas.

Soil mapping has been conducted in most countries globally, but they have typically extended only 1 or 1.5 meters into the soil, as such mapping of subsoils are demanding and have not been considered important. This makes such data of limited value to estimate the real potential of having crop roots grow deeper. Even for common crops with limited rooting depth, understanding the soil potential for deep rooting is considered important for estimating yield potentials [99]. Novel methods may allow us to map deep soil conditions on a larger scale, as in the global estimates of the depth of porous soil layers made by Pelletier *et al.* [100]. Such mapping can be of great value to understand where potentials for deep rooting exists, but it shows only one of the several important soil factors and needs to be combined with information on other important factors. If more such global or regional mapping were done, it would greatly assist our evaluation of the potential of deep rooting of crops. It can help us understand the overall potential, to define regions where deep rooting is especially promising, and help direct deep root research to areas where it has potential, or areas where we are trying to understand the actual severity and consequences of deep soil constraints.

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In spite of this potential for deep rooting, the effective rooting depth (i.e., where significant uptake of water and nutrients occur) of the most commonly grown crops is usually between 0.5 and 1.5 m [17]. Global food crop production is dominated by wheat, maize, rice, and soybean, sometimes referred to as 'the big four', and among them, only winter wheat reportedly reaches rooting depths greater than 1.5 m. Thus, the restricted rooting depth of most common arable crops results in little or no use of resources at depth. The main reason for this difference is the short growing season of annual crops, of typically 3 to 11 months depending on crop species and use. This limits the time needed for deep root development. Comparing the winter and spring varieties of wheat revealed that an extra 6 months, even though much of it was winter, doubled the final rooting depth [18].

In contrast, natural ecosystems with mixed and mostly perennial plant communities have a much greater ability to build and maintain deep roots than annual crops. This is also true for perennial crops (e.g., lucerne) and tree crops, where, for example, Li *et al*. [19] showed that apple orchards could increase their rooting depth with c. 1 m per year, reaching 23 m after 22 years of growth. However, simply comparing maximum rooting depths between natural ecosystems and cropping systems can be misleading. Permanent plant stands maintain deep rooting throughout the year, while annual crops only reach their maximum rooting depths towards the end of each crop cycle. This leads to a much lower average soil volume exploitation over a full year than suggested by the recorded maximum crop rooting depths (Figure 1; [20]).

In conclusion, current knowledge of deep roots of crops and wild plants shows that there is a potential to increase the growth of deep roots (i.e., extending the third dimension of agricultural

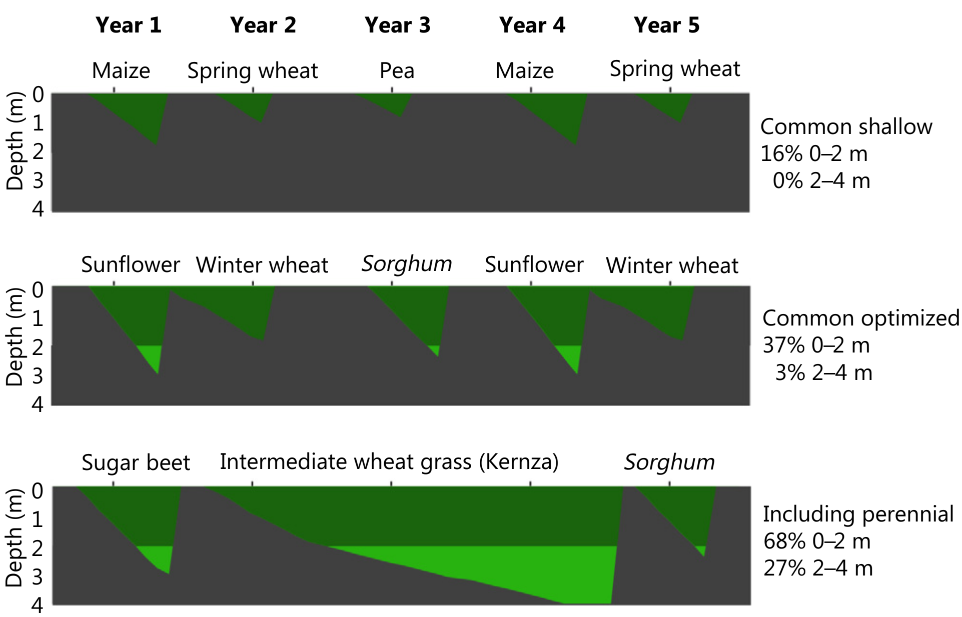

Figure 1. Diagram Illustrating Soil Exploitation by Crop Roots in Time and Depth of Three 5-Year Example Rotations, Assuming Typical Root Depth Development of the Crops, without Physical Barriers to Root Growth. The black areas of the figures indicate soil without active roots, the green areas soil with active roots. The dark green is rooted soil within the 0–2 m soil layer, the light green shows rooted soil in the 2–4 m soil layer. Integrated root occupancy is calculated as % of soil occupied by roots in time and space, in the 0–2 and 2–4 m soil layers. In example 1, common crops are chosen. Example 2 is also using common crops, but optimized by choosing deep-rooted species. In example 3, a perennial grain crop is included in three of the 5 years. The examples illustrate how markedly root exploitation by crops can be affected, even when relying on common crops, and the extra potential offered by including deep-rooted perennials. For an experimental example, see [18], where the effect of systematically including deep-rooted cover crops into a rotation is illustrated in a similar graph.

land). Improvements in the utilization of deeper soil resources could be achieved in various ways. It is clear that the most profound improvements may be reached by relying more on inherently deep rooted species (e.g., a shift from annual to perennial crop species [21]), though working to improve deep rooting of current crop species is more likely to bring significant improvements in the shorter term.

Do Crops with Deep Roots Acquire Resources in Deep Soil Layers?

While many studies document the widespread occurrence of deep rooting among plant species, there is much less information about acquisition of water and nutrients by deep roots. Access to water during prolonged dry periods is considered the most immediate benefit of deep roots, but uptake of nutrients can also be important (Figure 2).

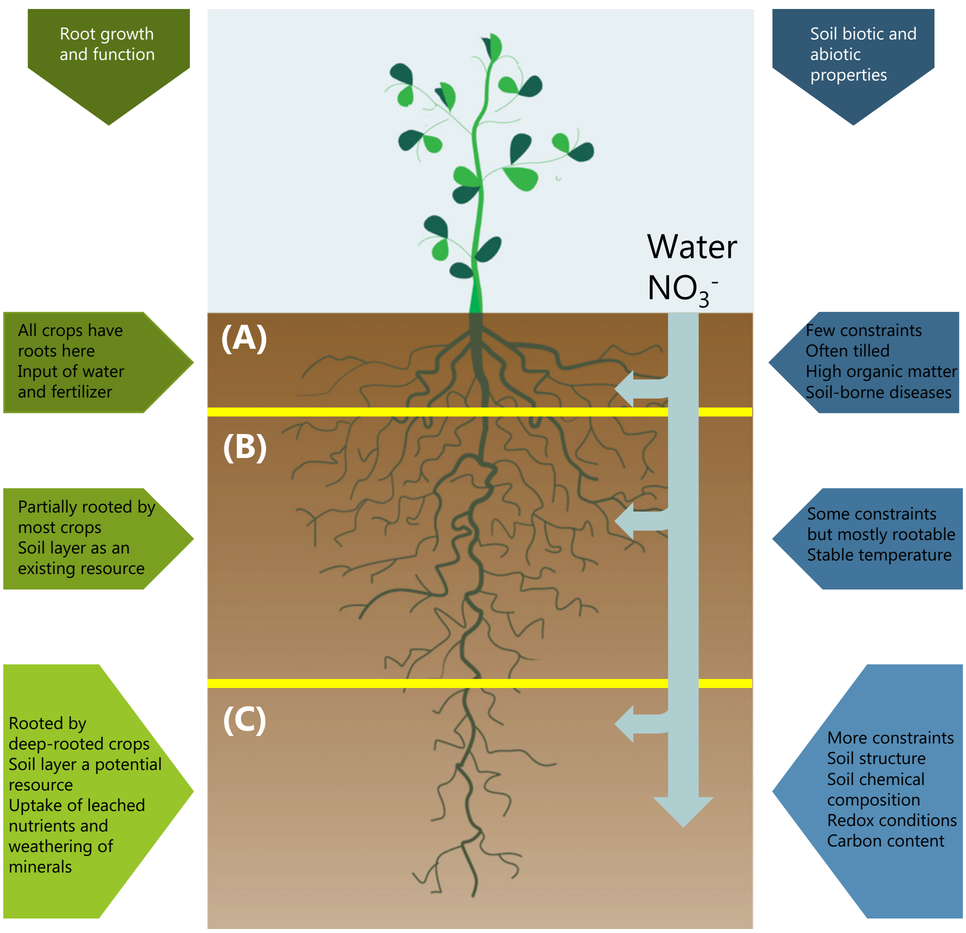

Figure 2. Root Growth and Function as Well as Soil Biotic and Abiotic Properties Will Vary down through the Soil Profile. (A) In the top soil (0–0.5 m), all crops will have high root density and meet few constraints. The content of organic matter is relatively high and any input of water and nutrients will be applied to this soil layer. Increasing the rooting density here will not affect the uptake of water and mobile nutrients significantly but may increase the uptake of immobile nutrients. (B) The next layer (0.5–1.5 m) is partially exploited by most crops, though roots are often active only for a short time in the later part of crop development. Nutrients and water are taken up from this layer, despite more constraints in soil abiotic properties than in the top soil. Increasing rooting depth and density will often increase the resource acquisition from this layer. (C) Below this zone, the soil is only rooted by deep-rooted crops, but is a potential resource for water and nutrients. Nutrient supply will either be derived from leaching through the soil or by weathering of minerals. This layer has more constraints against root growth due to soil structure, chemical composition, and redox conditions.

Deep-rooted crops can capture water otherwise lost to deep drainage, thus increasing water productivity in water-limited environments [22]. In an extreme case, apple trees 'mined' very deep soil water, as deep as 23 m in an environment with annual precipitation deficits [19], increasing the root depth and water mining with c. 1 m per year. Among herbaceous crops, lucerne is known to take up water to 5–10 m soil depth [23,24]; a young lucerne crop took up most of the water to 5 m soil depth within 2–3 years of growth. Among annual crops, although the maximum depth of water use is more limited, Stone *et al*. [25] showed substantial water use by sunflower to their maximum measurement depth of 3.1 m. Similarly, wheat has been shown to be able to use some water to 1.8 m depth [22,26]. Nielsen and Vigil [26] studied water extraction of a number of crops over 21 years and found evidence of soil water extraction down to 0.9, 1.2, 1.5, and 1.8 m for pea, millet, maize, and wheat, respectively.

Some nutrients, most notably nitrate, are rather mobile in the soil. Being very mobile, nitrate is often leached deep into the soil with percolating water altering deep soil nitrate concentrations [27,28], making nitrate available for acquisition by deep roots. Because of its mobility in water, nitrate can be acquired even at low root density. Significant nitrate acquisition from below 2 m depth has been shown in agricultural systems [10,29,30], reducing potential N leaching losses and eutrophication risks. In some cases, with cruciferous crops, depletion of available subsoil nitrate to 2.5 m was almost complete [31].

While the highest concentrations of most nutrients are generally found in the surface layers of agricultural soils, largely as a result of return of plant residues and application of fertilizers or organic amendments to the topsoil, a range of different plant-available nutrients were found at similar if not higher contents in the deep soil layers of arid and semiarid grasslands [32]. This was particularly the case for exchangeable Ca^{2+} and Mg^{2+}, which were higher below 1 m depth at all sites examined. Even though phosphorus (P) was mainly located in the surface soil, deeper soil layers also had significant concentrations. Actually, for both P and K, considerable reservoirs occur at depth in most soils as pools of P and K contained in poorly weathered minerals in both temperate [33] and tropical soils [34]. Significant nutrient acquisition from more than 2 m depth has also been shown in fast-growing eucalypt plantation trees, with the evidence of a greater capacity of deep roots for cation acquisition, compared with roots in surface layers [35,36]. In agricultural systems, Sr was taken up by lucerne from below 3 m depth [12].

Soil chemical and physical properties also vary between topsoils and subsoils. While topsoils often have higher organic matter and more available oxygen, subsoils can have more adverse pH, chemical, and biological conditions and less available oxygen due to the higher water content at depth [37]. Further, temperature and humidity conditions tend to be more stable in the subsoil, as it is not exposed to short-term weather fluctuations. However, roots and root exudates may considerably alter subsoil conditions and affect nutrient availability by weathering [34,38].

Can Deep Rooting of Agricultural Crops Be Improved?

Increased rooting depth of crops in current cropping systems may be achieved through a range of approaches, by plant breeding [39], or by various changes in crop management and optimization of crop rotations [40]. In the longer term, more radical improvements can be achieved by changing the crop species grown from annual to perennial, by intercropping shallow rooted crops with deeper rooted species, or by promoting agroforestry systems to ensure exploitation of deeper soil layers beneath the shallow rooted crops.

Breeding programs for deeper rooting are currently underway, though a main limitation is the lack of efficient and rapid phenotyping methods for deep rooting suitable for breeding programs [41].

Most attempts at larger scale phenotyping are applied to young plants or plants grown under laboratory conditions that are very different from field conditions. Despite this, some attempts at field phenotyping have been made [42,43] and genotypic differences in the order of 0.2–0.4 m in maximum rooting depth seem to be typical among comparable genotypes of the same annual crop species [44]. This may appear to be a limited range, but repeated cycles of breeding may lead to greater improvements than the current genetic variation indicates. In addition, deep rooting may have been counter-selected in major crops over the last decades of breeding for high-input agriculture; thus introgressing appropriate traits in modern germplasm may be worthwhile, as suggested for other root traits [45]. Further, breeding new deep-rooted genotypes is a highly efficient way to implement deeper rooting over large areas grown with a specific crop.

When trying to achieve deeper rooting, it is important to consider possible tradeoffs in root system architecture. Developing root systems optimized to reach deep soil layers fast (e.g., by breeding for a steep root angle in cereals [46]) may reduce the ability of the crop to exploit the topsoil at earlier stages of development [47]. Optimal rooting in upper soil layers is important and should not be compromised in the pursuit of deep rooting.

Exploiting the large differences among species in deep rooting may be the most promising long-term strategy to achieve cropping systems with overall deeper rooting. The variation among crop species is determined by a combination of differences in depth penetration rate and the duration of growth (e.g., [10]). Depth penetration seems to be an inherent trait if subsoil conditions allow growth, whereas branching and root density in deep soil layers is more plastic and dependent on resource availability. Based on the duration of growth, the potential of a shift from annual to perennial crops is evident, especially if species with high depth penetration rates can be selected (Figure 1). While crop choice is mainly governed by farm structure and market demand for crop products, there are still some obvious opportunities to change crop species. Currently, feed and bioenergy are mostly produced from annual grain crops and much of this could be substituted by perennial crops [48–50]. Moreover, future needs for crop biomass for biorefining [51,52] may provide opportunities to grow more perennial crops.

Crops grown for direct human consumption are more difficult to alter, but current efforts to develop perennial grain or oilseed crops [21,53] may in time result in a substantial conversion to perennial crop production. Strategies to develop perennial crops include *de novo* domestication of deep-rooted wild herbaceous perennial species [54] and wide hybridization between annual crop species and perennial relatives [55]. Both strategies have shown promise as a range of proto-crops move through the breeding pipeline [21], with the most advanced so far being perennial rice [56].

Fine-tuning of sowing time and depth represent crop management options to increase rooting depth. In addition, basic soil management can favor deep rooting, such as where drainage of wet soils is a well-established practice. Earlier sowing may significantly increase rooting depth of the crops if the total duration of crop growth is increased [57–59]. A recent study in Australia showed how access to slower maturing wheat cultivars, sown earlier and with greater access to deeper soil, could boost wheat yield by 25% and increase production by 7.1 Mt annually [60].

Improved crop rotations are well known to favor root health and thereby root development and function. While the direct effect on rooting depth has been rarely studied, improved uptake of subsoil water and nitrate has been documented [61]. In a long-term study, Sieling and Christen [62] showed that an improved rotation primarily increased wheat yields in dry growing seasons (i.e., when the crop relied more on deep water use). Crop rotation may also offer more sustainable soil improvements through deep rooting of succeeding crops by biopore formation. While most roots grow in established soil pores and cracks in the subsoil [63], roots of some plants have the ability to create new biopores in the subsoil through their root growth [64], promoting deep root development of subsequent crops [65,66].

Besides rotation, intercropping is another crop management strategy, which can increase the rooting depth of cropping systems and the soil volume exploited. In a walnut/wheat agroforestry system, roots of the walnut trees grew significantly deeper compared with pure stands of walnut trees, revealing the plasticity of root systems to avoid competition and access deep resources unavailable to the companion plants [67]. A similar effect of root over-yielding was found in mixed plantations of acacia and eucalypt relative to pure stands in deep, tropical soil conditions, in all soil layers down to the water table at a depth of 17 m [68]. Merely intercropping shallow rooted crops with more deeply rooted species will increase the soil volume explored by the combined crop mixture and thus the access to belowground resources.

Thus, a broad range of strategies are available to improve deep rooting in crop production, some relatively easy to implement in the short term, while others require substantial basic as well as on-farm adaptive research. Despite numerous papers that have demonstrated deep rooting and its potential benefits, we know far too little about this to confidently support on-farm practice changes, also because we need to know more about deep soil constraints towards deep root growth and function (Box 2). This arises from the practical challenges of studying deep rooting to improve our understanding of the likely contribution to crop water and nutrient supply, soil functioning, and system productivity in the longer term.

Can Deep Roots Contribute to Agricultural Productivity?

In principle, deep rooting will provide crops with access to increased reserves of otherwise unexploited soil water and nutrient resources. However, the values of the different resources vary strongly.

During periods with surplus precipitation, water and nutrients will leach downwards through the soil profile. While all nutrients to some extent can be transported, N and S dissolved in water as nitrate and sulfate anions are particularly mobile. Several aspects of growing annual crops on arable land favor this process [69]. Fertilizers are applied to increase nutrient availability to crops, but periods during which cropping is discontinued as well as shallow root growth of annual crops, favor water and nutrient losses from the topsoil. Following years of annual cropping, water and N contents can thus increase to several meters soil depth [27,70]. In medium and high rainfall areas, and especially on light textured soils, this mobility repeatedly replenishes the water and N available in deeper soil layers [71]. This makes water and N the two most agriculturally important soil resources to benefit from increased rooting depth.

The value of deep water and N depends on climate and soil conditions, which determine the amount and depth of water movement [72]. The value of deep water will be highest where the precipitation surplus is high enough to induce substantial percolation to depth, but where dry periods are sufficiently severe for deep water uptake to influence plant productivity [22,41]. This is important in crop production in many temperate areas with high autumn and winter rainfall and significant precipitation deficits during the main crop growth periods of spring and summer.

The amount of available water in deep soil layers can vary strongly with weather and soil conditions, but many examples quote water use of 100 to 200 mm from below 1 m by annual crops

[25,26]. In comparison, deeper rooted perennial crops have shown use of subsoil water of up to 5–10 m depth [23,24].

Based on general water productivity, an extra use of 1 mm of water will lead to a production of c. 50 kg extra biomass per hectare and increase cereal grain yield by 20–30 kg ha^{-1}. Considering typical deep soil water-holding capacity, this means that one extra meter of root depth could potentially add up to 4000 kg extra biomass production per hectare in case of water shortage. While the plants will need to invest C in achieving deeper rooting, deep root biomass is low compared with their potential value for biomass production. Deep water uptake may be of special value for grain yield as it is taken up by crops during late growth stages, and 1 mm of extra available subsoil water during grain filling under terminal stress in wheat can lead to a grain yield increase of over 50 kg ha^{-1} [22,58].

The amount of N available in the subsoil is even more variable than the amount of available water. Surplus and risk of nitrate leaching strongly depends on crop species [73], cropping systems, and intensity [74]. Unlike water, where soil porosity and field capacity set an upper limit to soil water content, there is no similar upper limit for N content. Studies have shown that deep rooted crops can deplete deep soil nitrate efficiently, reducing soil nitrate-N contents below 1 m depth by about 100 kg N ha^{-1} [10] within a short growth season. We do not know the limits to this, in depth or amount, but such results clearly show that increasing deep rooting of cropping systems can facilitate deep N acquisition and reduce the levels remaining in the subsoil that are at risk of leaching loss.

The presence of deep water and nitrate can to a large extent be predicted [58,72] and targeted strategies can be developed, where deep-rooted crops or cover crops are placed at critical positions within crop rotation, to recover what has been leached to deeper layers [10,75]. Cover crops offer a special opportunity where applicable, as the choice of cover crops is not limited by marketability, allowing farmers to choose deep-rooted species [76]. Such strategies may also be applied over longer time spans, where years of annual crops are followed by much deeper rooted perennial crops allowing ‘mining’ of water and N accumulated in the subsoil during the annual cropping phase (e.g., [19]).

For less mobile nutrients such as K and P, the value of deep rooting will typically be less critical for the individual crops, but may still be important for the sustainability of cropping systems, as it will increase the pool of available nutrients the cropping system can draw on. It will allow recovery of downwards leaching nutrients and nutrients stored in or weathered from the subsoil layers [77]. In specific situations, it will even be critical to growth and yield of individual crops, most obviously when nutrient acquisition from the topsoil is impaired by a dry topsoil.

Considering the need to develop more sustainable and high yielding cropping systems, deep rooting can play an important role. It may supply a substantial part of the nutrients required for crop production and it may allow us to keep crops adequately supplied with nutrients and attain high yields, while still keeping the nutrient losses to the environment at a low level, as has been shown for N [20]. Increased water use by crops will reduce water flows from farmland, with potential negative effects on the surrounding environment through less water supply to aquifers, but also positive effects where farmland evaporation is brought back closer to the evaporation of natural vegetation with deeper rooting.

Interactions between Deep Soil Biota and Roots

All crops grow in close connection with the soil biota, and the composition of the rhizosphere microbiome has been shown to significantly affect plant nutrition and health through both beneficial and pathogenic interactions [78]. Beneficial microbes mainly act by increasing nutrient availability, increasing plant resistance towards pathogens and suppressing pathogens in the soil. Recently, the impact on root growth of microbe–microbe interactions in the rhizosphere has been reported [79]. The prevalence of particular interactions depends on the composition of the microbial community in the soil matrix and at the root surface, the plant species/genotypes being responsible for a strong selection of the microbial community in its rhizosphere [80].

The microbial diversity in bulk soil has been shown to be significantly lower in the subsoil than in the topsoil [81] and the soil microbial community composition is affected by the physical and chemical properties of the soil. In subsoils, hypoxic or anoxic conditions are common, which alters the community structure [81]. In addition, differences in temperature, pH, nutrient, and organic carbon contents between topsoil and subsoil will affect the microbial and fauna community structures. The fungal:bacterial ratio decreases with soil depth, as does the presence of protozoans in soils [82]. In contrast, subsoils down to 70 cm depth containing root deposits have been shown to preferentially support growth of saprotrophic fungi [83]. Additionally, despite the higher abundance and species diversity in the topsoil, arbuscular mycorrhizal fungi have been found in subsoil layers down to 70 cm [84] and even down to 8 m depth in eucalypt plantations [85]. However, limited knowledge exists on the biota in deep soil layers and even less about rhizosphere microbial diversity and community composition below the topsoil. Hence, plant–microbe–fauna interactions in subsoils and their impact on crop health and growth still need to be untangled.

Expanding the root system to the subsoil will change the carbon regime of these deeper layers, driven by the succession of changes in response to the input of carbon from rhizodeposition and root turnover. The nitrogen acquisition of the deep rooted plants, the microbial degradation of freshly added organic matter, and the low oxygen diffusivity at high water contents may deplete oxygen and enhance denitrification [86], depending on the abundance of denitrifying microorganisms [87]. Enhancing denitrification in deep soil layers may contribute to reduced nitrate groundwater pollution, but also create low N availability affecting subsequent root growth as well as the carbon turnover and the stabilization processes.

Will Deep Rooting Improve Soil Quality and C Storage?

Globally, soil represents a reservoir of carbon twice as high as that of the atmosphere. Roughly half of the carbon stock is located in the topsoil (top 20 cm) and most of the soil organic carbon (SOC) is generally in the first meter of the soil profile, although some organic soils may have considerable carbon at larger depths [88]. The resilience of SOC increases with soil depth, as does the age of the organic compounds [89], as related to a lesser proportion of C of plant origin, and especially aboveground inputs, which occur predominantly in the topsoil [90]. There is evidence that SOC buried in deep soil layers (>1 m) may be stabilized for longer periods of time [91]; whether this also applies to carbon in deep soil deposited by plant roots is not yet clear.

Cropping systems with deep-rooted crops may enhance carbon input in deeper soil layers by growing deeper roots and root systems with a more equal root distribution down the soil profile [92,93]. This will result in deposition of fresh organic compounds in the deeper soil layers, where they will be subject to microbial decomposition. Nutrient availability is critical for the fate of deep-deposited C [94]. Low nutrient availability in deeper soil layers will affect the microbial turnover of fresh C inputs through rhizodeposition [95], often leading to priming effects, where the existing recalcitrant soil organic matter is decomposed by microorganisms to make its nutrients available for microbial communities [96]. This may ultimately lead to decomposition of otherwise protected subsoil carbon [97]. The risk of that may be particularly large in the part of the subsoil, where SOC is still sufficient to allow priming. In even deeper subsoil with very low

SOC, decomposition of added root C may be restricted by nutrient availability [98]. Thus, conditions for retention of added C from roots may depend greatly on C and nutrient availability in the specific soil horizons. It may even be needed for plants to bring essential nutrients (e.g., N) from topsoil layers to the subsoil to sustain microbial transformation processes leading to organic matter stabilization. These effects need to be explored under field conditions and over longer periods of time.

Concluding Remarks and Outlook

Existing research shows that the biological potential for extending the crop root zone deeper into the soil is substantial. It has been shown that deeper rooting leads to significant water and nutrient uptake and to carbon deposition in deeper soil layers, mostly left unexploited by current agricultural practice.

The total research on deep rooting is limited by the cost and challenges of studying processes deep in the soil. Thus, a range of topics related to physical, chemical, and biotic interactions between deep crop roots and the soil around them need further research. However, we believe that to understand the potential of deeper rooting as a tool towards sustainable intensification of crop production, the most critical priority will be research directed at quantification and upscaling of effects (see Outstanding Questions).

When we pursue deeper rooting through developing new or existing crops or their management, the important question is, how much this will contribute to uptake of water and nutrients, reduce leaching loss, and promote deep soil C sequestration across larger agricultural regions? In this work, the inherent potentials and limitations of different crop plants, which is the main focus of this paper, need to be combined with broader studies of the potentials and constraints of deep soils for root growth and function.

In doing so, it is important to leave behind any pre-assumption that deep roots are not important. Biologically, plants have developed the ability to form deep roots because of their value to the plants, and roots are adapted to deal with subsoil constraints, sometimes surprising us in what they can do!

Outstanding Questions

It has been documented that some crops can have significant root growth and function in deep soil layers, well below the 1–1.5 m maximum rooting depth of many common crops. However, most studies show examples and pinpoint potential, but fail to allow a broader overview of the potential of deeper rooting.

We need research that can broaden our current understanding of deep rooting and better quantify the potential contribution of deep rooting to improve sustainability of agricultural production on a larger scale.

Knowledge on strategies to achieve deeper rooting, by choosing or developing crops and their management, is required, as are better assessments of the contribution of deep rooting to water and nutrient uptake. Understanding, both spatially and temporally, how soil conditions limit rooting depth are also critical.

The main limit to our current knowledge is that existing methods for deep root research are expensive and highly demanding in terms of labor and technology and a common assumption that deep rooting is of limited importance.

The main research should then develop in three directions:

1) Methods to study deep root growth and functions: any contribution to develop less expensive methods, to allow more extensive or detailed studies will be of great value. Methods allowing dynamic studies and simultaneous observation of root growth and functions and effects on soil biota and soil C should be prioritized.
2) Potential of crops: wider comparative studies of crop species and genotypes, their root characteristics, and functions are needed to show how deep roots impact water and nutrient acquisition and C storage at depth. Deep root studies should develop beyond the few observations, to allow robust statistical analyses and allow for large-scale phenotyping and novel breeding strategies.

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3) Potential of deep rooting cropping systems for sustainable intensification: besides research directed at individual crops, research should address crop rotations and combinations of crops or genotypes with different rooting depth, from simple intercropping to agroforestry systems. Focus should be on how this may contribute to sustainable intensification of agriculture.

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