

Opinion

Root plasticity versus elasticity – when are responses acclimative?

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Spatiotemporal soil heterogeneity and the resulting edaphic stress cycles can be decisive for crop growth. However, our understanding of the acclimative value of root responses to heterogeneous soil conditions remains limited. We outline a framework to evaluate the acclimative value of root responses that distinguishes between stress responses that are persistent and reversible upon stress release, termed ‘plasticity’ and ‘elasticity’, respectively. Using energy balances, we provide theoretical evidence that the advantage of plasticity over elasticity increases with the number of edaphic stress cycles and if responses lead to comparatively high energy gains. Our framework provides a conceptual basis for assessing the acclimative value of root responses to soil heterogeneity and can catalyse research on crop adaptations to heterogeneous belowground environments.

Roots forage in heterogeneous environments

Spatial and temporal heterogeneity of soil properties and conditions define the environment of plant roots and can be decisive for crop growth. Adapting crops to soil heterogeneity is therefore key to the development of sustainable cropping practices [1–3]. The multiscale spatiotemporal heterogeneity of soils arises from the interplay between plants; soil physical, chemical, and biological properties, and processes; climatic conditions; and soil management [4–8]. The complex arrangement of solids and pores, known as ‘soil structure’, leads to spatial variability in soil bulk density, water and nutrient availability, and the composition and activity of the soil (micro)biome [3,9–12]. Since spatial variabilities of soil properties and conditions typically occur at the micrometre to centimetre scale, these heterogeneities affect individual plants at the root system and single-root level [2,12,13]. Precipitation and evapotranspiration patterns, root growth and exudation, water and nutrient uptake by plants, the activity of heterotrophic soil life, and soil structure dynamics collectively induce spatially explicit temporal fluctuations of soil conditions [11,14–19]. Such temporal fluctuations of environmental conditions in soil occur within hours to weeks [2,17] and are therefore relevant during the relatively short life cycle of arable plants. Agricultural soil management, including tillage, fertilisation, and irrigation, further modifies soil conditions in space and time [20,21]. Hence, arable plants must explore spatiotemporally heterogeneous environments to forage for water and nutrients.

Other than the idea of finding root ideotypes adapted to particular edaphic stresses [22,23], leveraging the ability of plants to adjust their root systems to specific edaphic conditions explicitly accounts for soil heterogeneity. Well-documented examples of such adjustments include root thickening upon greater soil bulk density [24], increased root growth towards and root proliferation in moist soil patches [25], and symbiosis with mycorrhizal fungi under poor nutrient availability [26]. The sum of root responses at the single-root level constitutes the root system response of an individual plant. Despite ample knowledge about the relevance of these root responses for soil exploration and resource uptake, the acclimative value of root responses for crop growth and yield

Highlights

Roots and associated soil biota are key to the energy balance of plants since they consume substantial amounts of photosynthates and in turn provide resources that fuel photosynthesis.

Due to spatiotemporal soil heterogeneity, single root systems are repeatedly exposed to soil conditions that either foster or limit plant growth.

Knowledge concerning the root responses to repeated cycles of edaphic stress remain scarce but is indispensable to understand root foraging behaviour in soil.

Quantification of the acclimative value of root responses to soil heterogeneity requires distinction between plastic (i.e., persistent) and elastic (i.e., reversible) root responses.

We introduce energy balances as an approach to capture the effects of repeated edaphic stress cycles on crop growth and yield formation and to quantify the acclimative value of root responses to specific soil environments.

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formation remains largely elusive. We argue this is due to the lack of a comprehensive understanding of root phenotypic responses that explicitly accounts for the spatiotemporal heterogeneities that characterize the majority of soil environments. In this opinion, we present a conceptual framework that facilitates the evaluation of the acclimative value of root responses to heterogeneous soil conditions using energy balances. To show the potential of the framework, we focus on three examples of root responses that cover root anatomical and architectural responses and interactions of plants with soil organisms: root thickening in response to high soil bulk density, root growth patterns upon heterogeneous water availability, and mycorrhiza formation under suboptimal phosphorus availability.

Scarce knowledge on root responses to repeated stress-release cycles

Root thickening is a commonly observed response to high soil bulk density [24], but the actual function of root thickening is not fully understood. Theoretical [27] and experimental evidence [28] suggests that thickening stabilizes roots against buckling, thereby preventing root failure, and thicker roots can develop more aerenchyma [29] to counteract poor aeration of dense soil [30]. Dense soil restricts ethylene diffusion out of the root into the bulk soil, leading to ethylene accumulation in and around the root tip [31]. Besides reducing root elongation rate [31,32], ethylene stimulates the biosynthesis of abscisic acid (ABA), which leads to radial expansion of root cortical cells and ultimately increases root diameter [33]. Roots sense water potential gradients in soil, allowing them to grow towards higher water availability. Such hydrotropic responses are mediated by asymmetric accumulation of ABA and asymmetric cell elongation in the cortex of the root elongation zone [34]. Hydropatterning, describing root branching towards moist soil, occurs upon differences in water availability across the circumferential root axis [35]. Higher auxin accumulation in the side of the root in contact with moist soil inhibits the formation of lateral root primordia on the side of the root that faces dry soil [36]. Ultimately, hydrotropism and hydropatterning allow efficient exploitation of soil water resources [25]. The mutualistic symbiosis between roots and arbuscular mycorrhizal fungi improves phosphorus acquisition by plants [26], and strigolactones play a central role in the establishment of root-fungal symbiosis. In response to phosphorus starvation, plants release strigolactones into soil [37]. Strigolactones act as chemical cues for the fungi to detect the host plant [38], stimulate hyphal branching in the vicinity of roots [39], and enhance penetration [40] and colonisation [41] of roots by mycorrhizal hyphae. Besides revealing molecular mechanisms underlying root responses to edaphic stresses, recent studies have identified genes linked to root thickening [31,33], hydrotropism [34,42], hydropatterning [35,36], and the formation of root-fungal symbiosis mediated by strigolactones [37,39–41].

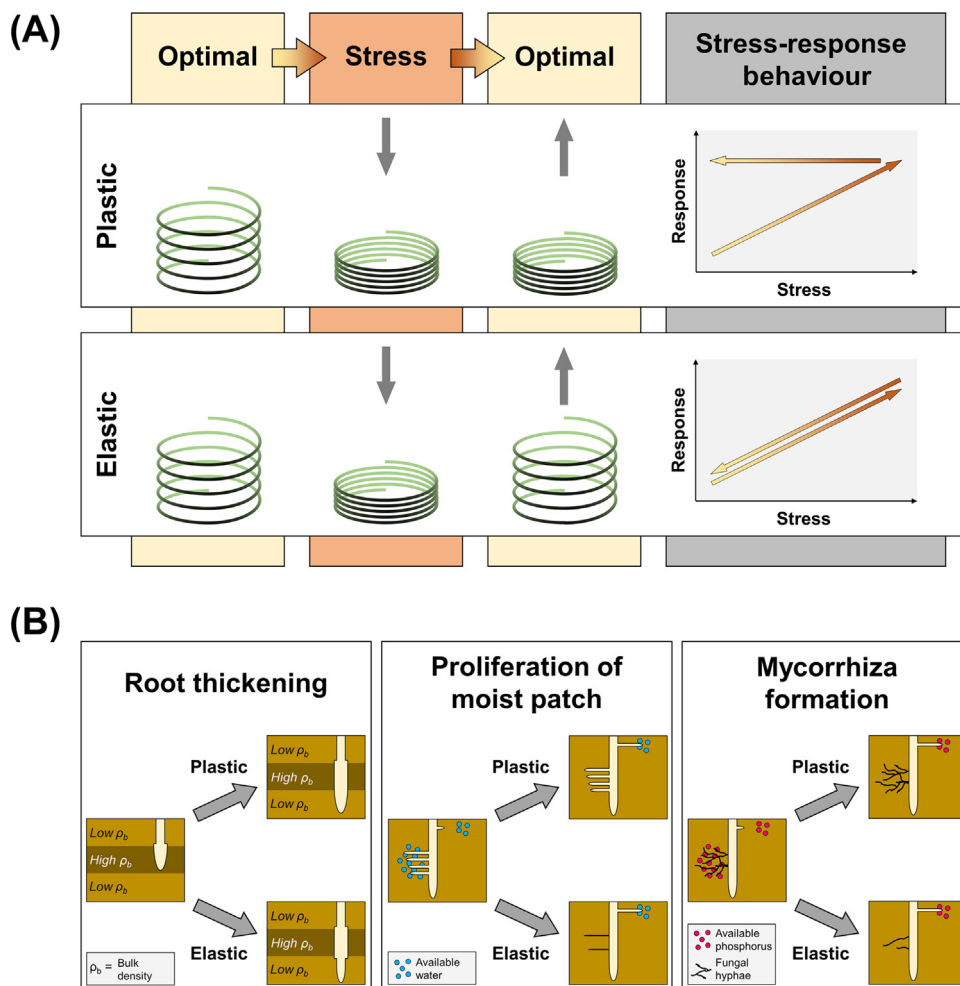
Spatiotemporal soil heterogeneity is perceived by plants as cycles of edaphic stress. Growing roots enter and leave denser and looser soil and repeatedly encounter zones with varying water and nutrient availability [1,2,12]. Wet–dry cycles frequently alter soil moisture distribution and thereby water and phosphorus availability, and resource uptake by plants and mycorrhizal fungi leads to localised resource depletion [5,17,19]. Hence, single roots and the entire root system of an individual plant are exposed to fluctuating environments. These fluctuations result in repeated stress-release cycles, and plant responses to a particular edaphic stress lose their function when the same stress is released. Root responses to the release of edaphic stress and the repeated re-exposure to the same stress are rarely addressed explicitly. Previous studies indicated that root thickening due to higher soil bulk density can persist or be reversed when roots re-enter looser soil [32,43–45]. However, the molecular processes underlying these phenotypic responses upon re-entry of looser soil remain unknown. Despite some indications for persistent and reversible root responses to fluctuating water availability [46–49], responses of lateral branching patterns and root-fungal symbiosis to spatiotemporal fluctuations in water and phosphorus availability are largely unknown. It remains to be investigated whether roots and

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mycorrhiza stay metabolically active or senesce upon localised depletion in water and phosphorus availability or upon increased resource availability in another patch explored by the same plant.

Rethinking root responses with classical mechanics

In classical mechanics, ‘plasticity’ describes deformation induced by an external stress that remains permanent after the stress is removed. ‘Elasticity’ describes deformation that is reversed upon stress release [50]. Hence, ‘plasticity’ and ‘elasticity’ refer to distinctly different stress-response behaviours of material (Figure 1A). Due to soil spatiotemporal heterogeneity, external stress is repeatedly applied to and released from roots during the life cycle of a plant. To explicitly



Trends in Plant Science

Figure 1. Soil heterogeneity and root stress-response behaviour. (A) Conceptual illustration of classical mechanics terminology to describe the different stress-response behaviours of roots to spatiotemporal heterogeneities of soil conditions. Root responses to edaphic stress are either persistent or reversible upon stress release, which indicates ‘plastic’ and ‘elastic’ stress-response behaviour, respectively. (B) Schematic representation of plastic and elastic stress-response behaviour of roots upon heterogeneity in soil bulk density and water and phosphorus availability. Persistent root thickening and root thinning upon re-entry into looser soil indicate plasticity and elasticity, respectively. Persistent metabolic activity of roots and mycorrhiza upon localised resource depletion and/or access to other water and nutrient pools indicate plasticity, whereas senescence of roots and mycorrhiza indicates elasticity.

account for these stress-release cycles, we propose a classical mechanics terminology to describe the stress-response behaviour of roots in soil. ‘Trait plasticity’ refers to root responses that persist after edaphic stress is released, whereas ‘trait elasticity’ refers to root responses that are reversed if the stress is released. Plasticity is exhibited if roots remain thicker upon re-entering looser soil and if lateral roots and mycorrhiza stay metabolically active after resources in their vicinity are depleted or if other parts of the same root system gain access to water and nutrients. Root thinning upon re-entering looser soil and the senescence of lateral roots and mycorrhiza in response to spatiotemporal changes in resource availability indicate elasticity (Figure 1B).

A bioenergetics perspective on acclimative root responses

Acclimative phenotypic responses to environmental stress (also referred to as ‘adaptive plasticity’ [51–54]) are defined as responses that improve plant fitness and thus the ability of an organism to spread its genes through reproduction [53,55]. However, the primary goal of agriculture is yield and not reproduction, and the two do not necessarily coincide. For example, a high germination rate is essential to reproductive success but not to grain yield. Similarly, reproductive success does not determine the yield of crops where vegetative or immature reproductive tissue is harvested, such as sugar beet, cassava, and grass or maize grown for silage. Hence, as highlighted previously [54], metrics other than fitness are needed to assess the acclimative value of root responses in arable crops.

Root growth and maintenance, root exudation, and root colonising symbionts such as mycorrhizal fungi may consume more than 50% of the energy plants acquire through photosynthesis [56–58]. In turn, roots and associated soil biota enable plants to access and extract water and nutrients, which are essential resources for photosynthesis and thus energy acquisition, crop performance, and yield formation (Figure 2A). Energy allocation to roots also fuels organisms that limit crop growth, such as belowground diseases and pests. Given this central role of roots for energy acquisition by plants [59], we propose using energy balances to evaluate the acclimative value of root responses to soil heterogeneity. Conceptually, the energy balance of an individual plant can be described as a function of time (t) as follows:

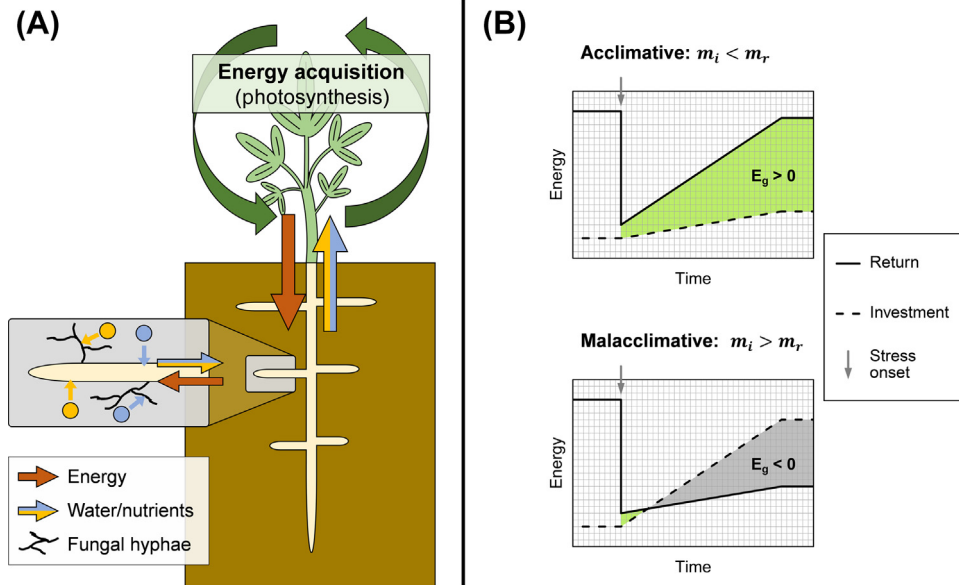
$$E_g(t) = \int E_r(t)dt - \int E_i(t)dt = \int [E_r(t) - E_i(t)]dt, \quad [1]$$

where E_g denotes the net energy gain, E_r denotes energy return (i.e. the contribution of resource uptake by roots and associated soil biota to photosynthesis), and E_i denotes energy investment into roots and associated soil biota. Equation 1 shows that E_r must outweigh E_i to achieve a net energy gain ($E_g > 0$).

Edaphic stress and thus soil conditions that limit resource access and uptake by plants, such as high soil bulk density and low water and nutrient availability, reduce photosynthesis and thus E_r . Typical responses to these adverse soil conditions, including root thickening [60,61], increased root growth and branching [62,63], and mycorrhiza formation [58,64,65], require greater energy allocation to roots, thereby increasing E_i . Besides increasing E_i , these root responses facilitate access and uptake of water and nutrients, which in turn increases E_r over time. The ratio between the temporal increase in E_r and E_i determines if a particular root response has acclimative value. If E_r increases at a higher rate than E_i , the associated root response results in a net energy gain ($E_g > 0$) and is therefore acclimative. Malacclimative responses, by contrast, are indicated by a net energy loss ($E_g < 0$), which occurs if E_i increases faster than E_r (Figure 2B).

The acclimative value of plastic and elastic stress-response behaviour

Root responses fostering soil exploration under edaphic stress require greater energy allocation to roots [58,60–65]. Hence, persistence and reversibility of root responses upon stress release



Trends in Plant Science

Figure 2. The role of roots and edaphic stress for the energy balance of an individual plant. (A) Plants invest energy into roots and associated soil biota (e.g., mycorrhizal fungi) to take up water and nutrients, which are essential to photosynthesis. This contribution of water and nutrient uptake to energy acquisition represents the energy return delivered by roots and associated soil biota. (B) With the onset of edaphic stress (grey arrow), water and nutrient uptake are reduced and energy return is decreased (unbroken line). In response, plants increase energy investment into roots (broken line) to fuel root responses that improve water and nutrient uptake (e.g., root thickening, increased branching, mycorrhiza formation) and thereby increase energy return. Root responses are acclimative if the temporal increase in energy investment (m_i) is smaller than the temporal increase in energy return (m_r), yielding a net energy gain ($E_g > 0$). Responses are malacclimative if m_i is larger than m_r , resulting in a net energy loss ($E_g < 0$).

that characterise plasticity and elasticity have distinct consequences for the energy balance of an individual plant. Following the bioenergetics perspective proposed here (Equation 1 and Figure 2), a higher net energy gain indicates greater acclimative value. For illustrative purposes and to demonstrate the implications of plasticity and elasticity for the acclimative value of root responses, we make the following assumptions and simplifications: (i) energy return decreases immediately with the onset of edaphic stress; (ii) energy return recovers immediately to prestress levels upon stress release; and (iii) the magnitude and temporal change of energy investment and return during stress exposure are the same under plastic and elastic behaviour.

The stress-release cycles experienced by roots consist of a period during which a particular edaphic stress occurs and a period during which the same stress is released. With the onset of the first exposure to edaphic stress, the energy return decreases. In response, plants increase energy investments into roots, which fuel root responses and ultimately lead to increasing energy returns (Figure 3A). Once the edaphic stress is released, the energy return recovers to prestress levels. If roots exhibit plastic behaviour, root responses persist when stress is released and energy investments do not return to prestress levels. Because of this persistence of root responses, roots are already adjusted upon reoccurrence of the same edaphic stress. Thus, with trait plasticity, the decrease in energy return in response to the reoccurrence of stress is smaller than for the initial stress occurrence (Figure 3A). Under elastic behaviour, energy return and energy investment recover to prestress levels when the stress is released due to the reversibility of root responses. Hence, with elasticity, temporal patterns of energy return and investment are consistent across multiple stress-

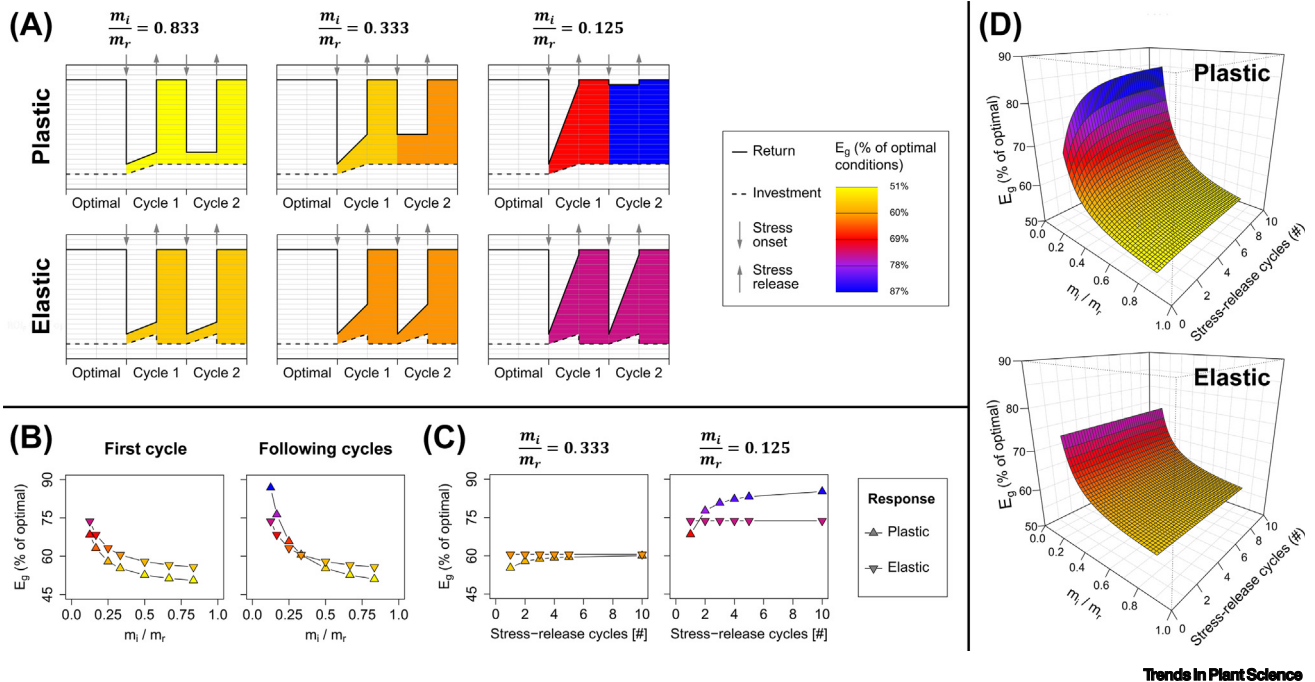


Figure 3. Schematic representation of the acclimative value of root trait plasticity and elasticity for the plant energy balance, expressed as the net energy gain (E_g ; see Equation 1 in the main text). (A) E_g for different ratios between the temporal increase in energy investment (m_i) and energy return (m_r) associated with a particular root response. (B) E_g as a function of m_i/m_r for the first and every following stress-release cycle. (C) E_g as a function of the number of stress-release cycles for $m_i/m_r = 0.333$ and $m_i/m_r = 0.125$. (D) Combined effect of m_i/m_r and the number of stress-release cycles on E_g , illustrating that the advantage of root plasticity over elasticity increases with lower m_i/m_r and/or higher number of stress-release cycles.

release cycles. Under plastic behaviour, by contrast, these patterns differ between the first and the following stress-release cycles (Figure 3A).

These differences in temporal patterns of energy return and investment between plasticity and elasticity have implications for the plant energy balance. Plasticity and elasticity yield the same net energy gain during the first period of stress exposure. Because of the reversibility of root responses, elasticity results in a higher net energy gain upon stress release than plasticity. Therefore, trait elasticity always yields greater net energy gain than trait plasticity during the first stress-release cycle (Figure 3B). Due to the persistence of root responses, trait plasticity yields higher net energy gains than trait elasticity during the period of stress exposure of every following stress-release cycle. Whether this effect of trait plasticity leads to higher net energy gains over an entire series of stress-release cycles depends on the ratio between the temporal increase in energy investment and return: The lower this ratio, the higher the benefit of trait plasticity for the plant energy balance (Figure 3B). Moreover, the advantage of plasticity over elasticity increases with the number of stress-release cycles (Figure 3C). Hence, plasticity bears greater acclimative value if a specific edaphic stress occurs frequently and/or if the resulting root response enables comparatively high energy return at low energy investment. Elasticity, however, has a higher acclimative value under infrequent stress occurrence and/or if a root response results in a comparatively low energy return (Figure 3D).

The theoretical considerations outlined here highlight that the dynamic interplay between plants and their belowground environment is the key factor that determines the acclimative value of different stress-response behaviours of roots in soil. Trait plasticity and elasticity have been indicated for

different root traits, including root diameter [32,43–45] and lateral branching patterns [46–49], and fluctuations in phosphorus availability appear to interfere with mycorrhizal symbiosis [66,67]. It is likely that conditions in arable soils will become more heterogeneous in the future. Management approaches to increase the sustainability of crop production, such as reduced tillage intensity [6,21] and reduced use of fertiliser [5], may lead to conditions resembling natural and thus more heterogeneous soil environments. Climate change and the concomitant increase in extreme weather events lead to greater soil moisture fluctuations within and between cropping seasons [68], which intensifies temporal heterogeneities of water availability, soil biological activity, and nutrient availability [69]. The framework presented here explicitly distinguishes between plastic and elastic root responses to repeated stress-release cycles and thereby allows capturing effects of soil heterogeneity on the plant energy balance. Hence, we provide a novel conceptual basis for understanding and assessing the acclimative value of root responses for crop growth and productivity.

Concluding remarks and future perspectives

Plants invest significant amounts of energy into their root system to ensure adequate water and nutrient uptake, which fuels energy acquisition of plants through photosynthesis. Therefore, the ratio between energy invested in roots and the contribution of roots to energy acquisition is crucial to the efficiency of root foraging behaviour in soil. Our framework highlights that different stress-response behaviour, namely trait plasticity and trait elasticity, can have distinct effects on the energy balance of plants. Combining heat dissipation measurements with root phenotypic assessments [60], plant growth measurements [60,70], and energy balance modelling [70,71] allows quantifying effects of environmental factors on energy allocation patterns in plants. X-ray [72,73], neutron [74,75], and near-infrared time-lapse imaging [76,77] provide opportunities for *in vivo* quantifications of root responses to spatiotemporal soil heterogeneities. Despite this availability of techniques and the wide recognition of the pivotal importance of soil heterogeneity for crop performance [1–3,5,8,9], knowledge on the effects of soil heterogeneity on energy allocation patterns in plants is scarce. Future studies that explicitly address stress-response behaviour of roots under heterogeneous soil conditions are essential to understand how plants forage for water and nutrients and to improve the efficiency with which crops explore soil (see [Outstanding questions](#)).

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Declaration of interests

The authors declare no competing interests.

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Outstanding questions

How can we design experimental systems that allow spatially explicit cycles of alternating edaphic stress and optimal growth conditions and simultaneous quantification of plant responses to such stress-release cycles?

What is the role of stress severity and stress frequency for stress-response behaviour of roots? Does the severity and frequency of edaphic stress influence whether plants exhibit plastic or elastic responses for a particular root trait?

What is the role of plant ontogeny for stress response behaviour of plant roots? How does the acclimative value of trait plasticity and elasticity change with the plant developmental stage and associated resource requirements?

How does the activity and composition of the soil (micro)biome influence stress-response behaviour of plant roots to repeated cycles of edaphic stress?

Does stress-response behaviour of roots to heterogeneous soil conditions reflect adaptations of different crop species and genotypes to particular soil environments?

How can plant breeders harness stress-response behaviour of roots to soil heterogeneity in order to adapt crop germplasm to specific soil environments, thereby increasing crop performance?

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