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Energy use efficiency of root growth – a theoretical bioenergetics framework

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ABSTRACT

Metabolic efficiency of root growth is a crucial physiological parameter, contributing to the amount of photosynthate that plants need to invest into soil exploration. Common measurements of metabolic efficiency usually rely on CO_2 respiration measurements with the underlying assumption that all metabolic processes are taking place under aerobic conditions. In this conceptual paper, we introduce energy use efficiency based on the quantification of heat dissipation and energy fluxes as an alternative metric to quantify the metabolic efficiency of root growth. In a theoretical framework, we adopted recently published heat dissipation data from wheat seedlings and show that energy use efficiency decreases in response to (i) soil hypoxia and (ii) increased soil penetration resistance. In contrast to traditional CO_2 respiration measurements, heat dissipation measurements account for both aerobic as well as anaerobic respiration in growing roots. Hence, we advocate that the quantification of heat dissipation provides a more complete picture of the metabolic efficiency of root growth than CO_2 respiration measurements alone. We therefore propose that energy use efficiency should be included in future studies assessing the metabolic efficiency of root growth.

Main text

Root growth is vital for plants to acquire water and nutrients but it requires substantial amounts of energy and thus photosynthate. Such an investment into belowground growth can significantly limit crop productivity, in particular under low soil fertility. Improving metabolic efficiency of root growth is therefore seen as a promising strategy to adapt crops to less fertile soils such as dry, flooded and compacted soils, and soils with low nutrient availability.[1,2] Metabolic efficiency is defined as the proportion between resources allocated to anabolic processes such as growth and catabolic processes such as respiration.[3] Usually metabolic efficiency is assessed by CO_2 respiration measurements, which relies on the assumption that all metabolic processes are occurring under aerobic conditions.[4] However, as soils are regularly hypoxic,[5–7] it is likely that the metabolism of growing roots is at least partially anaerobic. Recently, soil scientists have shown increased interest in quantifying the metabolic efficiency of soil microorganisms using a bioenergetics approach based on heat dissipation and energy fluxes.[4,8] Compared to CO_2 respiration measurements, heat dissipation recordings account for all metabolic processes. Metabolic efficiency is then expressed as energy use efficiency, referring to the proportion between energy allocated to anabolic processes such as growth and catabolic processes such as aerobic and anaerobic respiration.

In the conceptual framework presented here, we outline the use of energy use efficiency to assess the metabolic efficiency of root growth using soil hypoxia and high soil penetration resistance as case examples. Hypoxic conditions typically occur in flooded and dense soil, resulting in lower cellular oxygen concentration and a shift from aerobic to anaerobic respiration in the root growth zone.[9–11] Due to

this shift, cell division and cell elongation require greater amounts of energy (Figure 1). High penetration resistance characterizes dry and dense soil and imposes greater mechanical stress on the growing root tip, which increases the energy needed to penetrate soil[9,12,13] (Figure 1). Ultimately, low cellular oxygen concentration and high mechanical stress at the root tip increase the energy costs of root growth,[2,9] which decreases the energy use efficiency of root growth (Figure 1). We used recently published data on root growth and heat dissipation of wheat (*Triticum aestivum* L.) seedlings (n = 240) that were pre-germinated for 72 h followed by a 24 h growth period under three different levels of soil penetration resistance[2]. Energy allocated to all catabolic processes in the growing root (Q_c) was calculated as:

$$Q_c = Q_m \frac{1}{CR_{av}} CR_c \tag{1}$$

where Q_m [kJ] denotes the cumulative heat measured during 24 h by isothermal calorimetry[2]. CR_{av} represents the average calorespirometric ratio of carbohydrates such as glucose under *aerobic conditions* of 30 kJ g^{-1} CO_2-C. CR_c denotes the calorespirometric ratio of *all catabolic processes* in the growing root, which was set to either 30 kJ g^{-1} CO_2-C or 60 kJ g^{-1} CO_2-C to represent fully aerobic and partially anaerobic conditions, respectively.[14,15] A higher calorespirometric ratio resulted in increased Q_c, while soil penetration resistance did not affect Q_c (Figure 2a). Energy allocated to anabolic processes (Q_a [kJ]), i.e. root energy content, was calculated using the molar combustion enthalpy[16] ($\Delta H_{C\ gluc.}$ = 2813.6 kJ mol^{-1}), the molar mass ($M_{gluc.}$ = 180.16 g mol^{-1}) and the carbon content ($C_{gluc.}$ = 0.4 g g^{-1}) of glucose as:

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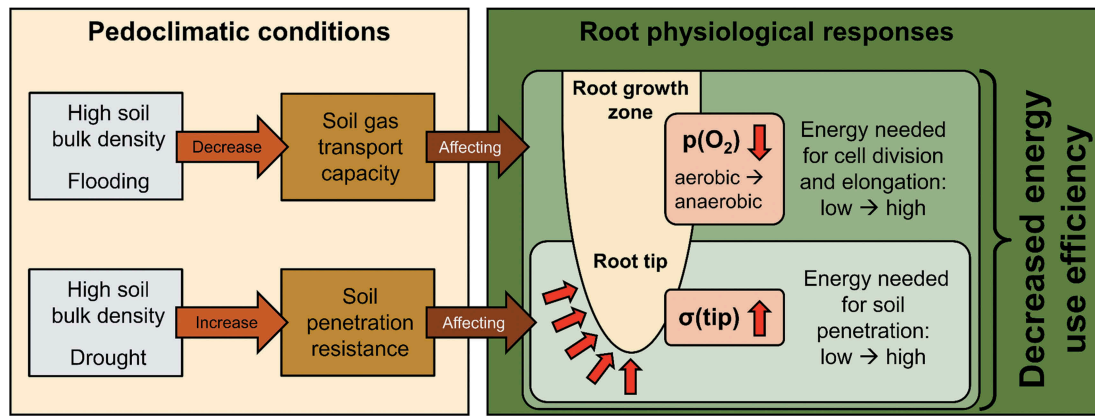
Figure 1. Conceptual overview illustrating relationships between pedoclimatic conditions and energy use efficiency of root growth. High bulk density and flooding decrease soil gas transport capacity, resulting in (i) decreased cellular oxygen concentration ($p(O_2)$) in the root growth zone and (ii) a shift from aerobic to anaerobic metabolism. Furthermore, high bulk density and drought increase soil penetration resistance, leading to higher mechanical stress at the growing root tip ($\sigma(tip)$). Energy requirements of root growth increase in response to low $p(O_2)$ and high $\sigma(tip)$, resulting in higher amounts of energy allocated to catabolic than anabolic processes and thus in a decrease of energy use efficiency.
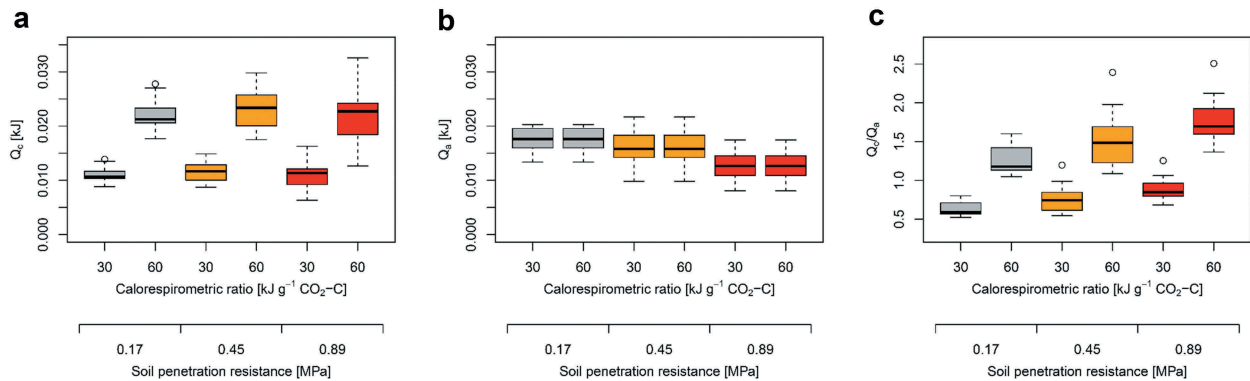

Figure 2. Effects of calorespirometric ratio and soil penetration resistance (PR) on (a) the energy allocated to root respiration (catabolic energy Q_c; Eq. 1), (b) the energy allocated to root growth (anabolic energy Q_a; Eq. 2), and (c) the ratio between Q_c and Q_a. Calorespirometric ratio of 30 and 60 kJ g^{-1} CO$_2$-C represent fully aerobic and partially anaerobic conditions, respectively. Calculations are based on mean values (n = 5) of 16 wheat genotypes taken from Colombi et al.[2].

$$Q_a = V_{bm}\rho_{bm}\frac{dw}{fw}C_{bm}\frac{\Delta H_{Cgluc}}{M_{gluc}C_{gluc}} \qquad (2)$$

where V_{bm} [cm^3] denotes root volume[2] and ρ_{bm} represents the tissue density of 1 g cm^{-3}. The ratio between root dry weight (dw) and root fresh weight (fw)[17] was set to 0.1 g g^{-1} and root carbon content (C_{bm})[18] was set to 0.38 g g^{-1}. Since Q_a is independent from the calorespirometric ratio and we assumed constant root biomass under aerobic and partially anaerobic conditions (Eq. 2), Q_a did not change upon increased calorespirometric ratio. However, Q_a decreased with increasing soil penetration resistance due to decreased root growth[2] (Figure 2b). Calculating the proportion between Q_c and Q_a shows how soil hypoxia and increased soil penetration resistance affect energy allocation. More energy was allocated to root respiration than to growth in response to soil hypoxia, i.e. upon an increase in the calorespirometric ratio, and upon greater penetration resistance (Figure 2c). Following previous definitions of metabolic efficiency[3], energy use efficiency (*EUE*) was then calculated as:

$$EUE = \frac{Q_a}{Q_c + Q_a} = \frac{Q_a}{Q_{tot}} \qquad (3)$$

Due to the increase of the proportion between Q_c and Q_a, energy use efficiency decreased by approximately 30% when the calorespirometric ratio increased from 30 kJ g^{-1} CO$_2$-C to 60 kJ g^{-1} CO$_2$-C. Accordingly, energy use efficiency decreased between 6% and 18% upon higher soil penetration resistance (Figure 3a). Moreover, energy use efficiency differed substantially among wheat genotypes (Table 1), indicating that there is genotypic diversity in energy use efficiency within a single species. As depicted in Eq. 3, the proportion of energy allocated to root growth (Q_a) relative to the total energy required for growth (Q_{tot}) decreases proportionally with energy use efficiency. Finally, carbohydrate-equivalents were derived from energy values using the molar combustion enthalpy of 2813.6 kJ mol^{-1} glucose. Using carbohydrate-equivalents, it becomes evident that plants need to invest more carbohydrates into root growth when energy use efficiency decreases (Figure 3b).

With this conceptual paper, we show that the metabolic efficiency of plant root growth can be assessed through the quantification of energy fluxes. Energy use efficiency is a suitable metric to determine the effects of soil hypoxia and increased soil penetration resistance on the metabolic costs of
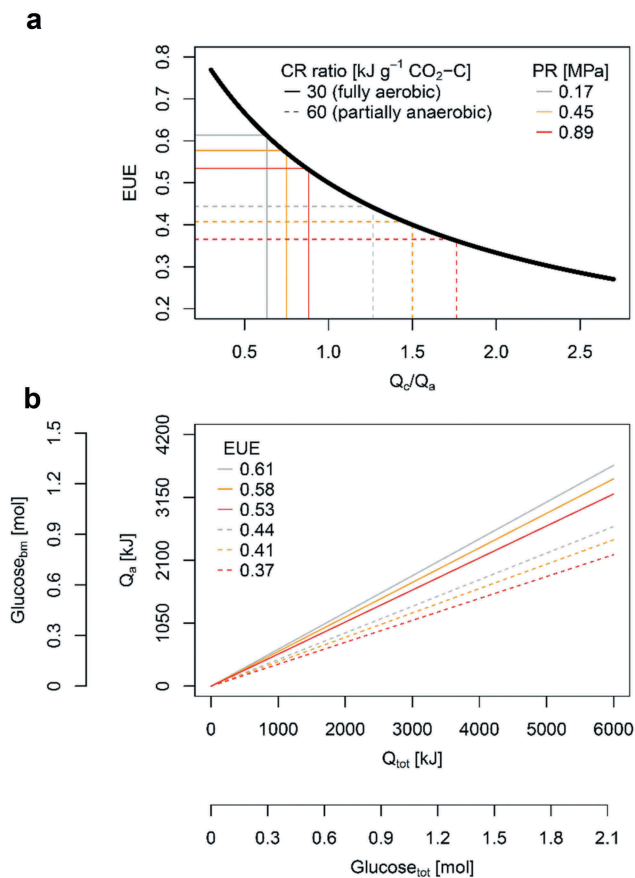
Figure 3. (a) Energy use efficiency (EUE; Eq. 3) as a function of the ratio between energy allocated to root respiration (catabolic energy Q_c; Eq. 1) and root growth (anabolic energy Q_a; Eq. 2) at different calorespirometric ratio (CR ratio) and levels of soil penetration resistance (PR). CR ratio of 30 and 60 kJ g^{-1} CO_2-C represent fully aerobic and partially anaerobic conditions, respectively. (b) Q_a as a function of the total energy required for root growth (Q_{tot}; Eq. 3) at different EUE. Carbohydrate equivalents for Q_a (Glucose$_{bm}$) and Q_{tot} (Glucose$_{tot}$) were calculated using the molar combustion enthalpy of 2813.6 kJ mol^{-1} glucose. CR ratio and soil penetration resistance are indicated by line style and color, respectively. All calculations are based on mean values of 16 wheat genotypes and five replicates (n = 80) taken from Colombi et al.[2]

Table 1. Summary statistics on energy use efficiency (EUE, Eq. 3) of root growth in wheat obtained from mean values (n = 5) of 16 wheat genotypes. Results are based on data presented in Colombi et al.[2]

CR ratio [kJ g^{-1} CO_2-C]	PR [MPa]	EUE			
		Min	Mean	Median	Max
30	**0.17**	0.555	0.614	0.629	0.656
	0.45	0.455	0.577	0.574	0.648
	0.89	0.443	0.534	0.541	0.594
60	**0.17**	0.385	0.444	0.459	0.489
	0.45	0.295	0.407	0.402	0.479
	0.89	0.285	0.366	0.371	0.423

Abbreviations: CR ratio = calorespirometric ratio, PR = soil penetration resistance, Min = genotype with lowest EUE, Mean = mean EUE across all genotypes, Median: median EUE across all genotypes, Max = genotype with highest EUE

soil exploration (Figure 3). The calorespirometric ratio associated with the metabolism in growing roots is a crucial parameter when determining energy use efficiency, particularly under hypoxic conditions. In the present framework, we assumed two theoretical calorespirometric ratios (Eq. 1; CR_c) to illustrate the effects of soil hypoxia on the metabolic efficiency of root growth. Similarly, we calculated the anabolic

energy allocated to root growth (Q_a), i.e. root energy content, based on root volume data, estimated root dry matter and carbon content, and the molar combustion enthalpy of glucose (Eq. 2). Our conceptual framework can therefore be further developed. The calorespirometric ratio of all catabolic processes in growing roots can be quantified directly by combining heat dissipation recordings with CO_2 respiration measurements.[4,14] Moreover, the energy content of roots can also be assessed using bomb calorimetry[19] together with measurements of root dry weight and root carbon content. In doing so, plant responses to soil-borne stress such as compaction, flooding or drought and their influences on energy use efficiency of root growth can be quantified directly.

Because soil hypoxia occurs regularly due to impeded gas exchange through the soil profile,[5–7] respiratory processes in roots are likely to be at least partially anaerobic. Hence, the most significant advantage of the proposed framework is that heat dissipation compared to traditionally used CO_2 respiration measurements accounts for both aerobic and anaerobic respiration processes. We therefore suggest that energy use efficiency should be considered when aiming to improve the metabolic efficiency of root growth.

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