

Letters

Carbon supply–consumption balance in plant roots: effects of carbon use efficiency and root anatomical plasticity

Introduction

The growth and maintenance of the plant root system may consume > 50% of all photosynthates, making the root system a major carbon sink (Lambers *et al.*, 2002). Carbon is supplied to roots via sieve tubes that are located in the phloem of the root stele, and is consumed for anabolic and catabolic processes. In a recent paper, Kong *et al.* (2021) proposed a framework to assess the carbon supply–consumption balance in plant roots that bridges root anatomical structures and root functioning using ‘structural allometric relationships’. Their framework highlights the pivotal role of root radius and associated anatomical properties such as sieve tube radius and the size and number of root cells for the carbon supply–consumption balance. Following the Hagen–Poiseuille law, they expressed root carbon supply rate (S) as:

$$S = k_s r_s^4 = k_s (k r_r)^4 \quad \text{Eqn 1}$$

where k_s denotes the coefficient of carbon flux rate, r_r denotes the root radius, and k denotes the scaling coefficient between the sieve tube radius (r_s) and r_r . Across plant species, the rate of root carbon consumption is strongly related to root radius, root cell number, and root cell size (Guo *et al.*, 2008; Lynch, 2015; Kong *et al.*, 2019). Kong *et al.* (2021) expressed total root carbon consumption rate (C_{tot}) as a function of root radius (r_r):

$$C_{\text{tot}} = k_c \pi r_r^2 \quad \text{Eqn 2}$$

where k_c denotes the carbon consumption rate per unit of root cross-sectional area.

Although not explicitly mentioned, the concept of carbon supply–consumption balance in roots presented by Kong *et al.* (2021) assumes that root metabolic processes are fully aerobic. Yet, soil oxygen concentration fluctuates strongly over time (Cannell *et al.*, 1984; Weisskopf *et al.*, 2010), and small-scale heterogeneities in soil porosity and water saturation and hotspots of soil biological activity can lead to localised differences in soil oxygen concentration (Ebrahimi & Or, 2018; Wang *et al.*, 2020). Therefore, a single root system and even a single root regularly encounter hypoxic and anoxic conditions, which may disrupt the carbon supply–consumption balance and the underlying structural

allometric relationships. Especially for annual plants such as arable crops, the spatial variability of soil properties, including soil oxygen concentration, may have decisive effects on whole plant growth (Wang *et al.*, 2020). In the present paper, we extend the framework of Kong *et al.* (2021) by including variations in oxygen concentration in the soil–root system and relating this to root anatomical plasticity. We then discuss how the presented approach may improve our understanding of the effects of spatial variability in oxygen concentration and other soil properties such as water and nutrient availability and soil penetration resistance on plant growth and crop yield formation.

Assessing the effects of soil oxygen on anabolic and catabolic carbon partitioning

Total carbon consumption in roots is the sum of anabolic processes, that is biosynthesis, and catabolic processes including respiration and fermentation (Bailey-Serres *et al.*, 2012; Lynch, 2015). With decreasing soil oxygen concentration, root metabolism gradually shifts from aerobic respiration towards anaerobic fermentation, and catabolic processes must increase to meet ATP demands of anabolic processes (Kennedy *et al.*, 1992; Bailey-Serres *et al.*, 2012). A few hours or days of hypoxia or anoxia, or a slight decrease in soil oxygen concentration can significantly affect root metabolism (Eavis, 1972; Leshuk & Saltveit, 1991; Garnczarska & Bednarski, 2004). Therefore, soil oxygen concentration affects carbon partitioning patterns between anabolic and catabolic processes in roots. The partitioning between anabolic and catabolic processes is often expressed as carbon use efficiency (Manzoni *et al.*, 2012), that is the ratio between anabolic and total carbon consumption rate (del Giorgio & Cole, 1998). Carbon use efficiency (e) of a root is therefore given by:

$$e = \frac{C_{\text{ana}}}{C_{\text{ana}} + C_{\text{cat}}} = \frac{C_{\text{ana}}}{C_{\text{tot}}} \quad \text{Eqn 3}$$

where C_{ana} denotes the carbon consumption rate of anabolic processes, and C_{cat} denotes the carbon consumption rate of catabolic processes including respiration and fermentation. In response to low soil oxygen concentration and the resulting decrease in cellular oxygen concentration, root catabolism gradually shifts from aerobic respiration to anaerobic fermentation (Fig. 1a). This metabolic shift can be described by the degree of anaerobicity (α). Fully aerobic metabolism is indicated by $\alpha = 0$, while $\alpha = 1$ indicates completely anaerobic metabolism. Following Chakrawal *et al.* (2020), carbon use efficiency can be related to the degree of anaerobicity by:

$$e = (1 - \alpha) Y_r + \alpha Y_f \quad \text{Eqn 4}$$

where Y_r represents carbon use efficiency of aerobic respiration and Y_f represents carbon use efficiency of anaerobic fermentation, which we set to 0.6 and 0.2, respectively (Manzoni *et al.*, 2012; Smeaton & Van Cappellen, 2018). Eqn 4 shows that carbon use efficiency decreases with decreasing soil oxygen concentration and the associated shift from aerobic respiration towards anaerobic fermentation. The proportion of catabolic and anabolic rates to total rate of root carbon consumption change then as follows:

$$C_{cat} = (1 - e) C_{tot} \quad \text{Eqn 5}$$

$$C_{ana} = e C_{tot} \quad \text{Eqn 6}$$

Upon a decrease in carbon use efficiency caused by a higher degree of anaerobicity, proportionally more carbon is allocated towards catabolic processes (Eqn 5; Fig. 1b) and less carbon is available for anabolic processes (Eqn 6). These effects of soil oxygen concentration on carbon use efficiency have immediate consequences for the carbon supply–consumption balance. If carbon

supply rate, and therefore total carbon consumption rate, of roots remain constant upon decreasing soil oxygen concentration, anabolic carbon consumption rate decreases. As a result, root biosynthesis decreases, which limits soil exploration, whole plant growth and crop productivity. Under decreased soil oxygen concentration, total carbon consumption rate and carbon supply rate must therefore increase to maintain anabolic carbon consumption rate of roots (Fig. 1c). However, increasing carbon supply rate reduces the amount of carbon available for aboveground plant growth and yield formation.

Integrating root anatomical plasticity into structural allometric relationships

As emphasised by Kong *et al.* (2021), total carbon consumption rate of roots does not only depend on root radius but it is also strongly influenced by root anatomical traits. Both, the enlargement of root cortical cells (Chimungu *et al.*, 2014; Colombi *et al.*, 2019) and cortical cell death (Saengwilai *et al.*, 2014; Schneider

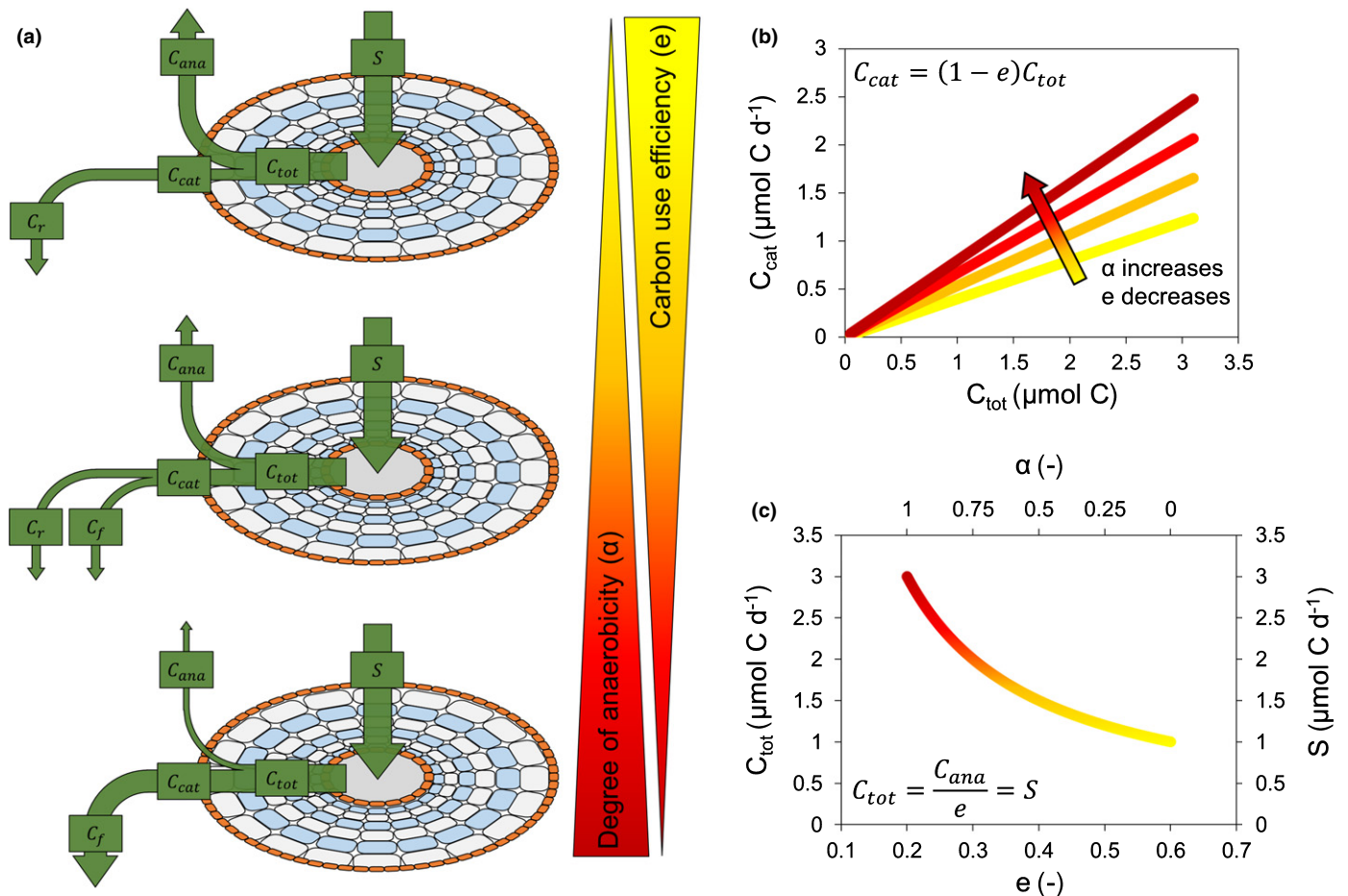


Fig. 1 Links between soil oxygen concentration and the rate of carbon supply (S) and consumption in plant roots. (a) Total root carbon consumption rate (C_{tot}) is the sum of anabolic carbon consumption rate (C_{ana}) and catabolic carbon consumption rate (C_{cat}) including aerobic respiration (C_r) and anaerobic fermentation (C_f). With decreasing soil oxygen concentration, the degree of anaerobicity (α) increases and root metabolism gradually shifts from respiration towards fermentation, which decreases carbon use efficiency (e) of roots (Eqns 3, 4). (b) C_{cat} as a function of C_{tot} , depicting the effects of decreasing soil oxygen concentration on the ratio between C_{cat} and C_{tot} (Eqn 5). (c) C_{tot} and S as a function of α and e , illustrating effects of decreasing soil oxygen concentration on relationships between S , C_{tot} , and C_{ana} (Eqn 6). Yellow-to-red colour scale denotes gradual change in carbon use efficiency from fully aerobic respiration ($\alpha = 0$, $e = 0.6$) towards fully anaerobic fermentation ($\alpha = 1$, $e = 0.2$).

et al., 2017) reduce the total carbon consumption rate of plant roots. Furthermore, low soil oxygen concentrations have been shown to increase root cortical cell size (Burgess *et al.*, 1999; Folzer *et al.*, 2006) and often induce cortical cell death (Kawase & Whitmoyer, 1980; Geisler-Lee *et al.*, 2010; Yamauchi *et al.*, 2014). Similar to changes in root metabolism (Eavis, 1972; Leshuk & Saltveit, 1991; Garnczarska & Bednarski, 2004), these root anatomical responses occur within hours to a few days of reduced soil oxygen concentration. Therefore, an approach that integrates these effects of root anatomical plasticity on carbon consumption rate of roots has to be adopted.

Adding a factor (f_{CS}) to Eqn 2, depicting the relative change of the average cross-sectional area of cortical cells (Δ_{CA}), enables to account for the effects of increasing cortical cell size on total root carbon consumption rate. Total carbon consumption rate of roots (C'_{tot}) is then given by:

$$C'_{tot} = C_{tot} f_{CS} = \frac{C_{ana}}{e} f_{CS} \quad \text{Eqn 7}$$

$$f_{CS} = \frac{1}{1 + \Delta_{CA}} \quad \text{Eqn 8}$$

When carbon is supplied at a constant rate, carbon supply–consumption balance can be reached at a carbon use efficiency of 0.45 and 0.3 by increasing cortical cell area by 33% ($f_{CS} = 0.75$) and 100% ($f_{CS} = 0.5$), respectively (Fig. 2a). The effect of cortical cell death on carbon consumption rate of roots can be accounted for by a factor (f_{CD}), describing the proportion between living cortical area (A_{liv}) and total cortical area (A_{tot}). Total carbon consumption rate of roots (C'_{tot}) can be related to cortical cell death as follows:

$$C'_{tot} = C_{tot} f_{CD} = \frac{C_{ana}}{e} f_{CD} \quad \text{Eqn 9}$$

$$f_{CD} = \frac{A_{liv}}{A_{tot}} \quad \text{Eqn 10}$$

Without increasing carbon supply rate, root carbon supply and consumption can be balanced at a carbon use efficiency of 0.45 and 0.3 by reducing the living cortical area by 25% ($f_{CD} = 0.75$) and 50% ($f_{CD} = 0.50$), respectively (Fig. 2b).

Several studies have shown that an increase in root cortical cell size or a reduction of living cortical area do not limit soil exploration, resource acquisition and whole plant growth (Chimungu *et al.*, 2014; Saengwilai *et al.*, 2014; Broughton *et al.*, 2015; Colombi *et al.*, 2019; Vanhees *et al.*, 2020). This indicates the importance of root anatomical plasticity in balancing root carbon supply and consumption rate without jeopardising above-ground growth. The enlargement of root cortical cells can coincide with a shift in cell shape towards cuboid-shaped cells (Folzer *et al.*, 2006), which increases intercellular gas space (Justin & Armstrong, 1987). Furthermore, cortical cell death may lead to the formation of root cortical aerenchyma (Pedersen *et al.*, 2021). Intercellular gas space and aerenchyma foster gas diffusion through roots (Justin & Armstrong, 1987; Pedersen *et al.*, 2021), which decreases the degree of anaerobicity. As a result, carbon use efficiency of roots

increases (Eqn 4) and a higher proportion of carbon can be allocated to anabolic processes (Eqn 6; Fig. 1). These feedbacks between root anatomy and physiology, and their effects on whole plant growth, highlight the need to integrate root anatomical plasticity into structural allometric relationships underlying the carbon supply–consumption balance in roots.

Outlook – linking root anatomical plasticity to soil heterogeneity

Soil oxygen concentration significantly controls the carbon use efficiency of roots (Fig. 1), which interferes with the balance between carbon supply and consumption rate in roots. Here we show that root anatomical plasticity may play a key role in the carbon supply–consumption balance of roots under hypoxic and anoxic conditions (Fig. 2). Other studies have indicated that this interplay between edaphic conditions, carbon use efficiency and root anatomical plasticity is not limited to soil oxygen concentration. Carbon use efficiency of heterotrophic soil microbes decreases under low nutrient availability (Manzoni *et al.*, 2017) and low soil moisture (Domeignoz-Horta *et al.*, 2020), and a decrease in carbon use efficiency of plant roots has been reported upon greater soil penetration resistance (Atwell, 1990; Colombi *et al.*, 2019). It is therefore likely that these edaphic stresses have similar effects on the root carbon supply–consumption balance as low soil oxygen concentration. Low nutrient and water availability, as well as high soil penetration resistance, can result in an increase in cortical cell size and a reduction of living cortical area, thereby decreasing root carbon consumption (Saengwilai *et al.*, 2014; Chimungu *et al.*, 2015; Colombi *et al.*, 2019; Vanhees *et al.*, 2020). Moreover, these anatomical adjustments can enhance nutrient and water acquisition (Lynch, 2019), which potentially increases the carbon use efficiency of roots. Therefore, root anatomical plasticity may play a crucial role in the carbon supply–consumption balance of plant roots under a variety of edaphic stresses.

Interactions between plants and heterotrophic soil organisms may further influence the carbon supply–consumption balance in roots. Mycorrhizas significantly contribute to root carbon consumption (Koide & Elliott, 1989; Kong *et al.*, 2021) and fungal colonisation can trigger root anatomical responses (Berta *et al.*, 1995; Deshmukh *et al.*, 2006; Lehr *et al.*, 2008). Similarly, changes in edaphic conditions and associated root anatomical responses can influence the colonisation of roots by mycorrhiza and pathogenic fungi (Vallino *et al.*, 2014; Galindo-Castañeda *et al.*, 2019). Furthermore, plants may alter carbon exudation, both in quantity and chemical composition, into the rhizosphere upon changing edaphic conditions (Rittenhouse & Hale, 1971; Boeuf-Tremblay *et al.*, 1995; Henry *et al.*, 2007; Williams & de Vries, 2020), which directly affects root carbon consumption. In addition to these direct effects, root exudation influences soil microbial communities and related biogeochemical processes (Hartmann *et al.*, 2009; York *et al.*, 2016; Yu *et al.*, 2021). Therefore, interactions between heterotrophic soil organisms colonising the root and the rhizosphere, root anatomy and root physiology are likely to alter the carbon supply–consumption balance in roots. Following the conceptual

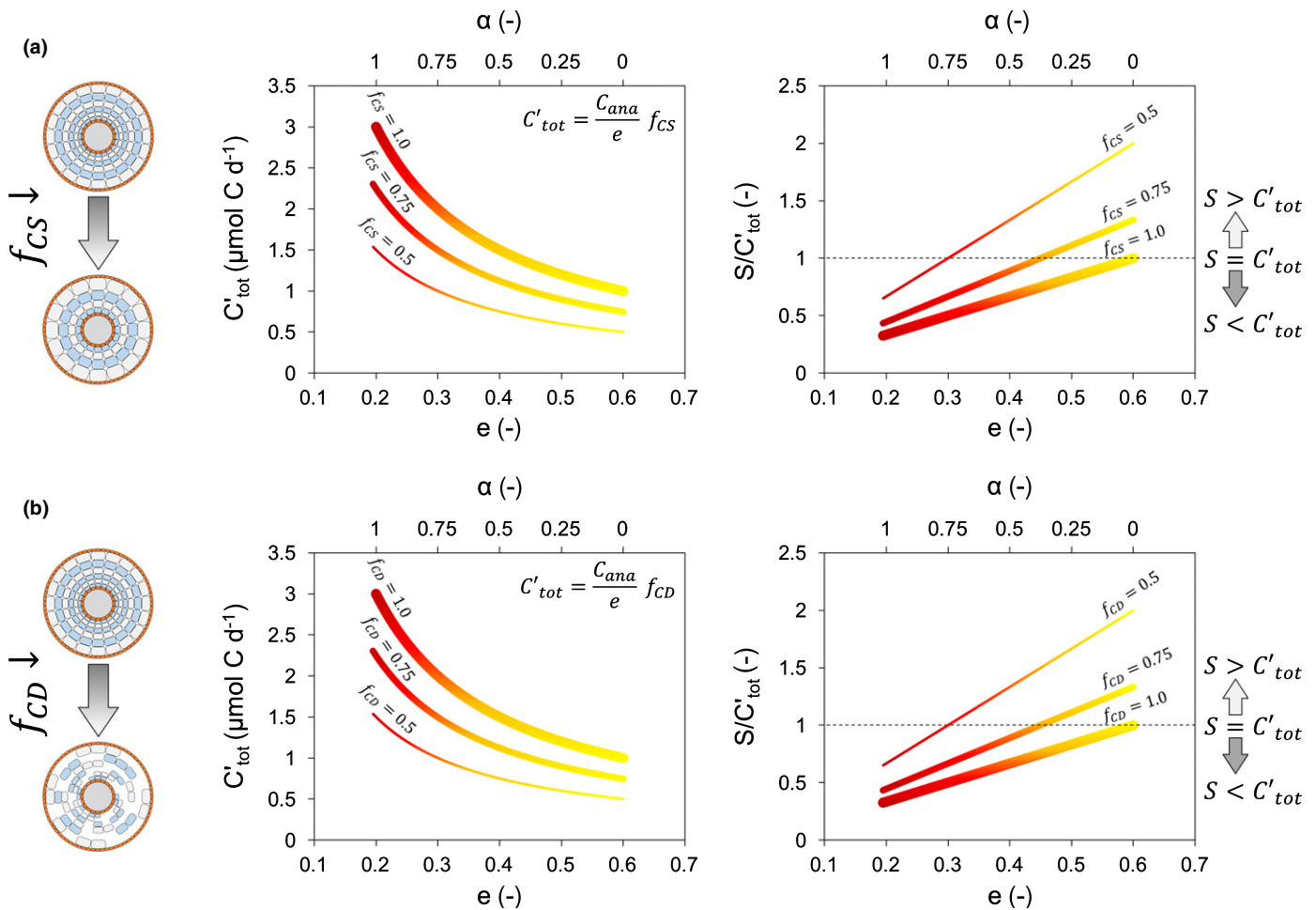


Fig. 2 Effects of root anatomical plasticity on the balance between carbon supply (S) and consumption (C'_{tot}) rate in plant roots under decreasing carbon use efficiency (e). (a) An increase of cortical cell area reduces C'_{tot} . An increase of the cortical cell area by 33% ($f_{CS} = 0.75$) and 100% ($f_{CS} = 0.5$) allows balancing S and C'_{tot} at $e = 0.45$ and $e = 0.3$, respectively, without a concomitant increase of S (Eqns 7, 8). (b) A reduction of living cortical area through cortical cell death reduces C'_{tot} . A reduction of living cortical area by 25% ($f_{CD} = 0.75$) and 50% ($f_{CD} = 0.5$) allows balancing S and C'_{tot} at $e = 0.45$ and $e = 0.3$, respectively, without a concomitant increase of S (Eqns 9, 10). Yellow-to-red colour scale denotes gradual change in carbon use efficiency from fully aerobic respiration ($\alpha = 0$, $e = 0.6$) towards fully anaerobic fermentation ($\alpha = 1$, $e = 0.2$).

approach outlined here, investigations into how these below-ground interactions affect carbon use efficiency of roots may improve our understanding of processes that underpin plant growth.

The heterogeneity of soil structure results in a large spatial variability of soil oxygen concentration, water and nutrient availability, soil penetration resistance and soil biological activity. It has been proposed that understanding plant responses to the spatial variability in soil properties will be key in the development of strategies to improve the sustainability of crop production (Wang *et al.*, 2020). Our conceptual approach shows how changes in soil properties may affect carbon use efficiency and ultimately the carbon supply–consumption balance in plant roots. Through root anatomical plasticity, plants may balance root carbon supply and consumption rate under changing edaphic conditions while maintaining soil exploration and aboveground plant growth. We therefore propose that the simultaneous assessment of root carbon use efficiency and root anatomical plasticity will provide new

insights into the effects of soil structural heterogeneity on plant growth. Performing such studies with different species and varieties has the potential to identify plant traits and belowground interactions that can be harnessed to enhance crop productivity.


Acknowledgements

Financial support from the Swedish Research Council for Sustainable Development (Formas; grant no. 2019-01189; grant number: 2017-00932), the Lantmännen Research Foundation (grant no. 2019H005), and the Swedish Research Council Vetenskapsrådet (grant no. 2016-04146) are gratefully acknowledged.


Author contributions

TC, AC and AMH developed the conceptual framework; TC wrote the manuscript with inputs from AC and AMH.

ORCID

Arjun Chakrawal  <https://orcid.org/0000-0003-4572-4347>

Tino Colombi  <https://orcid.org/0000-0001-8493-4430>

Anke Marianne Herrmann  <https://orcid.org/0000-0002-6273-1234>

Tino Colombi^{1*} , **Arjun Chakrawal^{2,3}**  and **Anke Marianne Herrmann¹** 

¹Department of Soil & Environment, Swedish University of Agricultural Sciences, PO Box 7014, Uppsala 75007, Sweden;

²Department of Physical Geography, Stockholm University, Svante Arrhenius Väg 8C, Frescati, Stockholm 10691, Sweden;

³Bolin Centre for Climate Research, Stockholm University, Stockholm 10691, Sweden

(*Author for correspondence: email tino.colombi@slu.se)

References

- Atwell BJ. 1990. The effect of soil compaction on wheat during early tillering. III. Fate of carbon transported to the roots. *New Phytologist* 115: 43–49.
- Bailey-Serres J, Lee SC, Brinton E. 2012. Waterproofing crops: effective flooding survival strategies. *Plant Physiology* 160: 1698–1709.
- Berta G, Trotta A, Fusconi A, Hooker JE, Munro M, Atkinson D, Giovannetti M, Morini S, Fortuna P, Tisserant B *et al.* 1995. Arbuscular mycorrhizal induced changes to plant growth and root system morphology in *Prunus cerasifera*. *Tree Physiology* 15: 281–293.
- Boeuf-Tremblay V, Plantureux S, Guckert A. 1995. Influence of mechanical impedance on root exudation of maize seedlings at two development stages. *Plant and Soil* 172: 279–287.
- Broughton S, Zhou G, Teakle NL, Matsuda R, Zhou M, O'Leary RA, Colmer TD, Li C. 2015. Waterlogging tolerance is associated with root porosity in barley (*Hordeum vulgare* L.). *Molecular Breeding* 35: 27.
- Burgess T, Hardy GESJ, McComb JA, Colquhoun I. 1999. Effects of hypoxia on root morphology and lesion development in *Eucalyptus marginata* infected with *Phytophthora cinnamomi*. *Plant Pathology* 48: 786–796.
- Cannell RQ, Belford RK, Gales K, Thomson RJ, Webster CP. 1984. Effects of waterlogging and drought on winter wheat and winter barley grown on a clay and a sandy loam soil – I. Crop growth and yield. *Plant and Soil* 80: 53–66.
- Chakrawal A, Herrmann AM, Šantrůčková H, Manzoni S. 2020. Quantifying microbial metabolism in soils using calorimetry – a bioenergetics perspective. *Soil Biology and Biochemistry* 148: 107945.
- Chimungu JG, Brown KM, Lynch JP. 2014. Large root cortical cell size improves drought tolerance in maize (*Zea mays* L.). *Plant Physiology* 166: 2166–2178.
- Chimungu JG, Maliro MFA, Nalivata PC, Kanyama-Phiri G, Brown KM, Lynch JP. 2015. Utility of root cortical aerenchyma under water limited conditions in tropical maize (*Zea mays* L.). *Field Crops Research* 171: 86–98.
- Colombi T, Herrmann AM, Vallenback P, Keller T. 2019. Cortical cell diameter is key to energy costs of root growth in wheat. *Plant Physiology* 180: 2049–2060.
- Deshmukh S, Hüchelhoven R, Schäfer P, Imani J, Sharma M, Weiss M, Waller F, Kogel KH. 2006. The root endophytic fungus *Piriformospora indica* requires host cell for proliferation during mutualistic symbiosis with barley. *Proceedings of the National Academy of Sciences, USA* 103: 18450–18457.
- Domeignoz-Horta LA, Pold G, Liu X-JA, Frey SD, Melillo JM, DeAngelis KM. 2020. Microbial diversity drives carbon use efficiency in a model soil. *Nature Communications* 11: 3684.
- Eavis BW. 1972. Soil physical conditions affecting seedling root growth. *Plant and Soil* 36: 613–622.
- Ebrahimi A, Or D. 2018. Dynamics of soil biogeochemical gas emissions shaped by remolded aggregate sizes and carbon configurations under hydration cycles. *Global Change Biology* 24: e378–e392.
- Folzer H, Dat JF, Capelli N, Rieffel D, Badot PM. 2006. Response of sessile oak seedlings (*Quercus petraea*) to flooding: an integrated study. *Tree Physiology* 26: 759–766.
- Galindo-Castañeda T, Brown KM, Kuldau GA, Roth GW, Wenner NG, Ray S, Schneider H, Lynch JP. 2019. Root cortical anatomy is associated with differential pathogenic and symbiotic fungal colonization in maize. *Plant, Cell & Environment* 42: 2999–3014.
- Garczarska M, Bednarski W. 2004. Effect of a short-term hypoxic treatment followed by re-aeration on free radicals level and antioxidative enzymes in lupine roots. *Plant Physiology and Biochemistry* 42: 233–240.
- Geisler-Lee J, Caldwell C, Gallie DR. 2010. Expression of the ethylene biosynthetic machinery in maize roots is regulated in response to hypoxia. *Journal of Experimental Botany* 61: 857–871.
- del Giorgio PA, Cole JJ. 1998. Bacterial growth efficiency in natural aquatic systems. *Annual Review of Ecology and Systematics* 29: 503–541.
- Guo D, Xia M, Wei X, Chang W, Liu Y, Wang Z. 2008. Anatomical traits associated with absorption and mycorrhizal colonization are linked to root branch order in twenty-three Chinese temperate tree species. *New Phytologist* 180: 673–683.
- Hartmann A, Schmid M, van Tuinen D, Berg G. 2009. Plant-driven selection of microbes. *Plant and Soil* 321: 235–257.
- Henry A, Doucette W, Norton J, Bugbee B. 2007. Changes in crested wheatgrass root exudation caused by flood, drought, and nutrient stress. *Journal of Environmental Quality* 36: 904–912.
- Justin SHFW, Armstrong W. 1987. The anatomical characteristics of roots and plant response to soil. *New Phytologist* 106: 465–495.
- Kawase M, Whitmoyer RE. 1980. Aerenchyma development in waterlogged plants. *American Journal of Botany* 67: 18.
- Kennedy RA, Rumpho ME, Fox TC. 1992. Anaerobic metabolism in plants. *Plant Physiology* 100: 1–6.
- Koide R, Elliott G. 1989. Cost, benefit and efficiency of the vesicular-arbuscular mycorrhizal symbiosis. *Functional Ecology* 3: 252–255.
- Kong D, Wang J, Wu H, Valverde-Barrantes OJ, Wang R, Zeng H, Kardol P, Zhang H, Feng Y. 2019. Nonlinearity of root trait relationships and the root economics spectrum. *Nature Communications* 10: 2203.
- Kong D, Wang J, Valverde-Barrantes OJ, Kardol P. 2021. A framework to assess the carbon supply–consumption balance in plant roots. *New Phytologist* 229: 659–664.
- Lambers H, Atkin O, Millenaar F. 2002. Respiratory patterns in roots in relation to their functioning. In: Waisel Y, Eshel A, Kafkaki K, eds. *Plant roots, hidden half*. New York, NY, USA: Marcel Dekker Inc, 521–552.
- Lehr NA, Schrey SD, Hampp R, Tarkka MT. 2008. Root inoculation with a forest soil streptomycete leads to locally and systemically increased resistance against phytopathogens in Norway spruce. *New Phytologist* 177: 965–976.
- Leshuk JA, Saltveit ME. 1991. Effects of rapid changes in oxygen concentration on the respiration of carrot roots. *Physiologia Plantarum* 82: 559–568.
- Lynch JP. 2015. Root phenes that reduce the metabolic costs of soil exploration: opportunities for 21st century agriculture. *Plant, Cell & Environment* 38: 1775–1784.
- Lynch JP. 2019. Root phenotypes for improved nutrient capture: an underexploited opportunity for global agriculture. *New Phytologist* 223: 548–564.
- Manzoni S, Čapek P, Mooshammer M, Lindahl BD, Richter A, Šantrůčková H. 2017. Optimal metabolic regulation along resource stoichiometry gradients. *Ecology Letters* 20: 1182–1191.
- Manzoni S, Taylor P, Richter A, Porporato A, Ågren GI. 2012. Environmental and stoichiometric controls on microbial carbon-use efficiency in soils. *New Phytologist* 196: 79–91.
- Pedersen O, Sauter M, Colmer TD, Nakazono M. 2021. Regulation of root adaptive anatomical and morphological traits during low soil oxygen. *New Phytologist* 229: 42–49.
- Rittenhouse RL, Hale MG. 1971. Loss of organic compounds from roots. *Plant and Soil* 35: 311–321.
- Saengwilai P, Nord EA, Chimungu JG, Brown KM, Lynch JP. 2014. Root cortical aerenchyma enhances nitrogen acquisition from low-nitrogen soils in maize. *Plant Physiology* 166: 726–735.
- Schneider HM, Postma JA, Wojciechowski T, Kuppe C, Lynch JP. 2017. Root cortical senescence improves growth under suboptimal availability of N, P, and K. *Plant Physiology* 174: 2333–2347.

- Smeaton CM, Van Cappellen P. 2018. Gibbs energy dynamic yield method (GEDYM): predicting microbial growth yields under energy-limiting conditions. *Geochimica et Cosmochimica Acta* 241: 1–16.
- Vallino M, Fiorilli V, Bonfante P. 2014. Rice flooding negatively impacts root branching and arbuscular mycorrhizal colonization, but not fungal viability. *Plant, Cell & Environment* 37: 557–572.
- Vanhees DJ, Loades KW, Bengough AG, Mooney SJ, Lynch JP. 2020. Root anatomical traits contribute to deeper rooting of maize under compacted field conditions. *Journal of Experimental Botany* 71: 4243–4257.
- Wang X, Whalley WR, Miller AJ, White PJ, Zhang F, Shen J. 2020. Sustainable cropping requires adaptation to a heterogeneous rhizosphere. *Trends in Plant Science* 25: 1194–1202.
- Weisskopf P, Reiser R, Rek J, Oberholzer HR. 2010. Effect of different compaction impacts and varying subsequent management practices on soil structure, air regime and microbiological parameters. *Soil and Tillage Research* 111: 65–74.
- Williams A, de Vries FT. 2020. Plant root exudation under drought: implications for ecosystem functioning. *New Phytologist* 225: 1899–1905.
- Yamauchi T, Watanabe K, Fukazawa A, Mori H, Abe F, Kawaguchi K, Oyanagi A, Nakazono M. 2014. Ethylene and reactive oxygen species are involved in root aerenchyma formation and adaptation of wheat seedlings to oxygen-deficient conditions. *Journal of Experimental Botany* 65: 261–273.
- York LM, Carminati A, Mooney SJ, Ritz K, Bennett MJ. 2016. The holistic rhizosphere: integrating zones, processes, and semantics in the soil influenced by roots. *Journal of Experimental Botany* 67: 3629–3643.
- Yu P, He X, Baer M, Beirinckx S, Tian T, Moya YAT, Zhang X, Deichmann M, Frey FP, Bresgen V *et al.* 2021. Plant flavones enrich rhizosphere Oxalobacteraceae to improve maize performance under nitrogen deprivation. *Nature Plants* 7: 481–499.

Key words: carbon use efficiency, edaphic stress, phenotypic plasticity, root carbon balance, soil heterogeneity.

Received, 7 April 2021; accepted, 29 June 2021.



About New Phytologist

- *New Phytologist* is an electronic (online-only) journal owned by the New Phytologist Foundation, a **not-for-profit organization** dedicated to the promotion of plant science, facilitating projects from symposia to free access for our Tansley reviews and Tansley insights.
- Regular papers, Letters, Viewpoints, Research reviews, Rapid reports and both Modelling/Theory and Methods papers are encouraged. We are committed to rapid processing, from online submission through to publication 'as ready' via *Early View* – our average time to decision is <23 days. There are **no page or colour charges** and a PDF version will be provided for each article.
- The journal is available online at Wiley Online Library. Visit **www.newphytologist.com** to search the articles and register for table of contents email alerts.
- If you have any questions, do get in touch with Central Office (np-centraloffice@lancaster.ac.uk) or, if it is more convenient, our USA Office (np-usaoffice@lancaster.ac.uk)
- For submission instructions, subscription and all the latest information visit **www.newphytologist.com**

See also the Commentary on this article by Valverde-Barrantes, 233: 1539–1541.