INSTITUT FÜR NUTZPFLANZENWISSENSCHAFTEN UND RESSOURCENSCHUTZ (INRES) LEHRSTUHL FÜR PFLANZENBAU

Field-based evidence of root plasticity under abiotic stresses and tillage

Dissertation

zur Erlangung des Grades

Doktorin der Agrarwissenschaften (Dr. agr.)

der Agrar-, Ernährungs- und Ingenieurwissenschaftlichen Fakultät
der Rheinischen Friedrich-Wilhelms-Universität Bonn

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Quito - Ecuador

Bonn, 2026

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Tag der mündlichen Prüfung: 01.12.2025

Angefertigt mit Genehmigung der Agrar-, Ernährungs- und Ingenieurwissenschaftlichen
Fakultät der Universität Bonn

Dedicatory

When I reflect on what I need to be truly happy, three essential pillars come to my mind.

First, I need motivation. Someone who inspires me to become a better version of myself every single day. That motivation is my daughter, Marcela. My precious princess, this achievement is for you. You are the light that guides me each morning, and I would change the world for you.

Equally important is having someone to admire. A person who embodies persistence, resilience, strength, and unconditional love. That person is my mother, Gina. This accomplishment is also for you, with all my love and deepest gratitude.

Finally, happiness would not be complete without someone who grounds me, walks beside me through every step of the journey, and helps bring dreams to life. That person is my husband, Wladimir, my beloved partner. Thank you for always being there. This achievement is for you as well.

Acknowledgments

First, I want to thank Prof. Dr. Sabine Seidel, my supervisor. From the first day, she guided every step of my work; planning trials and field sampling, organizing logistics, reading drafts, writing papers, and helping me publish. Just as important, she listened when things were difficult and always found time for another question or a quick talk. Her steady support kept me moving forward.

I am grateful to the PhenoRob project for funding my position and providing the equipment, resources, and training that good research requires.

Sincere thanks go to Jun. Prof. Dr. Janina Dierks and Prof. Dr. Gabriel Schaaf for serving on my examination committee and reviewing my thesis. I am especially grateful to Prof. Dr. Gabriel Schaaf and Dr. Johannes Auke Postma for many thoughtful discussions on nutrient stress and root biology that helped shape key parts of my research.

I would also like to thank Dr. Amit Srivastava, whose kind words and fresh ideas helped me stay confident in my work.

Warm thanks to Dr. Ixchel Hernández, colleague and friend, for her sharp scientific feedback and for brightening long days with her humor and style.

I am deeply grateful to Dr. Clara Bazzo for her generous support during my research visits. Her hospitality made it possible for me to carry out experimental work under challenging conditions.

Thanks also to everyone in the Crop Science Group at INRES, especially our head, Dr. Thomas Gaiser, for open doors, shared knowledge, and honest feedback. Fieldwork would not have been possible without the dedication of Dr. Hubert Hüging, Phillip Nachtweide, and Milena Ulrich; their effort in cold, hot, and muddy conditions helped bring this work to completion.

To my family and friends in Germany, Luxembourg, and Ecuador: thank you for the many wonderful moments that kept me optimistic and grounded during this journey. To my husband, my mother, my brother, and my niece: your love, patience, and faith in me made this possible. Every page of this thesis carries a piece of your support.

List of further publications

- Hadir, S., **Lopez**, G., Seidel, S., Nyameasem, J., Bauke, S., & Hernandez-Ochoa, I. (2025). Winter rye root growth and plasticity in response to nitrogen and phosphorus omission under field conditions. *Plant Soil*, 518. https://doi.org/10.1007/s11104-025-08088-w.

- Yi, J., **Lopez**, G., Hadir, S., Weyler, J., Klingbeil, L., Deichmann, M., Gall, J., & Seidel, S. J. (2025). Non-invasive diagnosis of nutrient deficiencies in winter wheat and winter rye using UAV-based RGB images. *Computers and Electronics in Agriculture*, 239. https://doi.org/10.1016/j.compag.2025.110865.

- Dreier, A., **Lopez**, G., Bajracharya, R., et al. (2025). Structural wheat trait estimation using UAV-based laser scanning data: Analysis of critical aspects and recommendations based on a case study. *Precision Agric*, 26, 18. https://doi.org/10.1007/s11119-024-10202-4.

- Nguyen, T., **Lopez**, G., Seidel, S., Lärm, L., Bauer, F., Klotzsche, A., Schnepf, A., Gaiser, T., Hüging, H., & Ewert, F. (2024). Multi-year aboveground data of minirhizotron facilities in Selhausen. *Scientific Data*, 11. https://doi.org/10.1038/s41597-024-03535-2.

- Lärm, L., Bauer, F., Hermes, N., Kruk, J., Vereecken, H., Vanderborght, J., Nguyen, T., **Lopez**, G., Seidel, S., Ewert, F., Schnepf, A., & Klotzsche, A. (2023). Multi-year belowground data of minirhizotron facilities in Selhausen. *Scientific Data*, 10. https://doi.org/10.1038/s41597-023-02570-9.

- Srivastava, A. K., Safaei, N., Khaki, S., **Lopez**, G., Zeng, W., Ewert, F., Gaiser, T., & Rahimi, J. (2022). Winter wheat yield prediction using convolutional neural networks from environmental and phenological data. *Scientific Reports*, 12(1), 3215. https://doi.org/10.1038/s41598-022-06249-w.

Summary

Modern crop production must meet rising food demand while avoiding further losses of soil fertility, water, and biodiversity. However, intensive tillage, chronic shortages of nitrogen (N), phosphorus (P), or potassium (K), and emerging climate pressures such as higher temperatures, shifting rainfall, and more frequent drought continue to erode soils and reduce yields, threatening both food security and the land's capacity to store carbon. Roots lie at the center of this dilemma: they secure water and nutrients, stabilize soil, and mediate below-ground carbon inputs, yet their form and function shift with each stressor and with management choices such as conventional versus conservation tillage. Despite this importance, most field studies of root traits are scarce because they are technically demanding, and widely used crop–soil models do not consider the plasticity that governs real root-to-shoot interactions. Quantifying how nutrient deficits, tillage regimes, drought, warming, and elevated CO_2 reshape root–shoot allocation, and testing whether current simulation tools can capture those responses, form the central challenge that this thesis explores.

The first systematic review synthesizes 50 field experiments that tracked how major crops adjust their root systems when N, P, or K is deficient. The meta-analysis shows that N and P shortages shorten total root length by approximately 9% and 14% and shrink root biomass by 7% and 25%, yet they also steer more growth below ground: root length per unit shoot mass rises by 33% (N) and 51% (P), and the root-to-shoot ratio climbs under N stress in 44% of comparisons. Too few data were available to draw firm conclusions for K.

Second, a field experiment analyzes two seasons of winter wheat grown in the Dikopshof long-term fertilizer experiment to test how omission of N, P, K, or lime reshapes shoots and roots. Fully fertilized plots, with and without manure, produced the highest leaf area, shoot biomass, plant height, and grain yield. Omitting N or all fertilizer reduced those shoot traits and total root length or biomass but increased specific root length, the root-to-shoot ratio, and root length per unit shoot mass, indicating stronger below-ground investment under stress. Deficiency of P, K, or lime mainly reduced straw yield while often maintaining or extending root length, revealing trait-specific plasticity. Correlation and principal component analyses linked soil nutrient status closely to shoot vigor and root architecture.

The second systematic review analyzes 28 field experiments (117 paired observations) that compared conventional tillage (CT) with non-conventional systems, namely no-till or minimum tillage (NT), for their effect on the root-to-shoot ratio of 12 temperate crops. Averaged over all data, the mean root-to-shoot ratio did not differ significantly (0.22 in CT versus 0.29 in NT), but responses varied with crop and soil. Rapeseed and barley showed 2% and 15% higher ratios under NT, whereas maize and wheat had 2–6% higher ratios under CT; sandy soils favored higher ratios in CT (+8%) while clayey soils favored lower ratios in CT (16%). Sampling depth, years since NT adoption, soil bulk density, and seasonal rainfall explained much of the remaining scatter.

The final study links field evidence with modeling by examining how five abiotic factors (elevated CO_2, drought, nitrogen shortage, air-temperature shifts, and tillage) change the root-to-shoot ratio and how four soil-crop models (STICS, SIMPLACE, AgroC, and MONICA) simulate those changes in winter wheat. Meta-analysis shows that the ratio rises on average by about 12% with higher CO_2, 14% under drought, and 44% when soil N is low; tillage has little overall effect except for a 15% increase in wheat, while warming responses are highly variable and often negative (mean 48%). Models capture the small CO_2 and tillage effects but undervalue drought and N effects and disagree sharply on temperature, revealing large structural uncertainty in carbon allocation routines.

Across all four studies, a common pattern emerges: nutrient shortages, particularly N and P, and drought shift more biomass below ground, elevating the root-to-shoot ratio; higher temperature often lowers that ratio; tillage effects are small and context dependent; and elevated CO_2 offers only modest gains. These results highlight where current crop–soil models still rely on fixed allocation rules and shallow rooting depths. Future work should broaden the database by running multi-site nutrient-omission (especially P and K) and warming trials, pairing in-situ measurements of root exudates with morphology, and calibrating models with high-frequency root data and improved stress-specific routines for carbon allocation so that they can track dynamic partitioning and deep-root carbon inputs with less uncertainty.

Zusammenfassung

Moderne Nutzpflanzenproduktion muss die steigende Nachfrage nach Nahrungsmitteln decken und zugleich weitere Verluste an Bodenfruchtbarkeit, Wasser und Biodiversität vermeiden. Doch intensive Bodenbearbeitung, chronische Engpässe bei Stickstoff (N), Phosphor (P) oder Kalium (K) sowie neue Klimaeinflüsse wie höhere Temperaturen, veränderte Niederschlagsmuster und häufigere Dürreperioden setzen den Böden weiter zu und mindern die Erträge, was sowohl die Ernährungssicherheit als auch die Kohlenstoffspeicherkapazität der Böden gefährdet. Wurzeln stehen im Zentrum dieses Dilemmas: Sie erschließen Wasser und Nährstoffe, stabilisieren den Boden und lenken Kohlenstoff in tiefere Schichten, verändern jedoch ihre Form und Funktion je nach Stressfaktor und Bewirtschaftungsform (z. B. konventionelle vs. konservierende Bodenbearbeitung). Trotz ihrer Bedeutung sind Feldversuche zu Wurzeleigenschaften selten, weil sie technisch aufwendig sind und gängige Boden-Pflanzen-Modelle die Plastizität, die reale Wurzel-Spross-Interaktionen steuert, nicht berücksichtigen. Die zentrale Aufgabe dieser Arbeit besteht daher darin, zu quantifizieren, wie Nährstoffdefizite, Bodenbearbeitung, Trockenheit, Erwärmung und erhöhtes CO_2 das Wurzel-Spross-Verhältnis beeinflussen, und zu prüfen, ob aktuelle Simulationsmodelle diese Reaktionen abbilden können.

Die erste systematische Übersichtsarbeit fasst 50 Feldversuche zusammen, in denen untersucht wurde, wie wichtige Nutzpflanzen ihr Wurzelsystem bei N-, P- oder K-Mangel anpassen. Die Metaanalyse zeigt, dass N- und P-Knappheit die Gesamtwurzellänge um etwa 9 % bzw. 14 % verkürzt und die Wurzelbiomasse um 7 % bzw. 25 % verringert, gleichzeitig jedoch das Wachstum in den Boden verlagert: Die Wurzellänge pro Sprossmasse steigt um 33 % (N) bzw. 51 % (P), und das Wurzel-Spross-Verhältnis nimmt in 44 % der Vergleiche unter N-Stress zu. Für K lagen zu wenig Daten vor, um belastbare Aussagen zu treffen.

Ein anschließender Feldversuch untersucht Winterweizen über zwei Vegetationsperioden auf dem Dauerdüngungsversuch Dikopshof, um zu untersuchen, wie der Entzug von N, P, K oder Kalk Spross und Wurzeln beeinflusst. Parzellen mit Volldüngung, mit und ohne Stallmist, erzielten die höchste Blattfläche, Sprossbiomasse, Pflanzenhöhe und den höchsten Kornertrag. Der Verzicht auf N oder auf sämtliche Düngung verringerte diese Sprossmerkmale sowie die Gesamtwurzellänge bzw. -biomasse, erhöhte jedoch die spezifische Wurzellänge, das Wurzel-Spross-Verhältnis und die Wurzellänge je Sprossmasse; ein Hinweis auf eine stärkere Investition in unterirdische Pflanzenorgane unter Stress. P-, K- oder Kalkmangel minderte vor allem den Strohertrag, während die Wurzellänge häufig konstant blieb oder zunahm, was eigenschaftsspezifische Plastizität offenlegt. Korrelations- und Hauptkomponentenanalysen zeigten eine enge Verbindung zwischen Sprossvitalität und Wurzelarchitektur mit dem Nährstoffstatus des Bodens.

Die zweite systematische Übersichtsarbeit wertet 28 Feldversuche (117 Paarvergleiche) aus, in denen konventionelle Bodenbearbeitung (CT) konservierender Bodenbearbeitung, also Direktsaat oder Minimalbodenbearbeitung (NT), gegenübergestellt

wurde. Im Mittel unterschied sich das Wurzel-Spross-Verhältnis nicht signifikant (0,22 bei CT vs. 0,29 bei NT), die Reaktionen variierten jedoch je nach Kulturart und Boden. Raps und Gerste zeigten ein 2 % bzw. 15 % höheres Verhältnis unter NT, während Mais und Weizen unter CT 2–6 % höhere Wurzel-Spross-Verhältnisse aufwiesen; sandige Böden begünstigten höhere Verhältnisse bei CT (+8 %), tonige Böden niedrigere (–16 %). Probentiefe, Jahre seit NT-Einführung, Bodendichte und saisonaler Niederschlag erklärten einen Großteil der Streuung.

Die letzte Studie verbindet Felddaten mit Modellierung, indem sie untersucht, wie fünf abiotische Faktoren (erhöhtes CO_2, Trockenheit, Stickstoffmangel, Temperaturschwankungen und Bodenbearbeitung) das Wurzel-Spross-Verhältnis verändern und wie vier Boden-Pflanzen-Modelle (STICS, SIMPLACE, AgroC, MONICA) diese Änderungen bei Winterweizen abbilden. Die Metaanalyse zeigt durchschnittliche Anstiege des Verhältnisses um etwa 12 % bei höherem CO_2, 14 % unter Trockenheit und 44 % bei niedrigem Bodenstickstoff; Bodenbearbeitung hat insgesamt wenig Einfluss, außer einem Anstieg um 15 % bei Weizen, während Erwärmungsreaktionen sehr variabel und oft negativ sind (Mittel –48 %). Die Modelle erfassen die kleinen CO_2- und Bodenbearbeitungseffekte, unterschätzen jedoch Trockenheit und N-Effekte und weichen bei Temperatur stark ab, was große strukturelle Unsicherheit in den Kohlenstoffallokationsroutinen offenlegt.

Über alle vier Studien hinweg zeigt sich ein einheitliches Muster: Nährstoffmangel, insbesondere an N und P, sowie Trockenheit verlagern mehr Biomasse in den Boden und erhöhen das Wurzel-Spross-Verhältnis; höhere Temperaturen senken dieses Verhältnis häufig; Effekte der Bodenbearbeitung sind klein und kontextabhängig; erhöhtes CO_2 bringt nur moderate Zugewinne. Diese Ergebnisse verdeutlichen, dass aktuelle Boden-Pflanzen-Modelle noch immer auf festen Allokationsregeln und geringen Wurzeltiefen basieren. Künftige Arbeiten sollten die Datenbasis erweitern, indem standortübergreifende Nährstoff-Auslass- (besonders für P und K) und Erwärmungsversuche durchgeführt werden, *in-situ*-Messungen von Wurzelexsudaten mit morphologischen Daten kombiniert und Modelle mit zeitlich hochaufgelösten Wurzeldaten sowie verbesserten stressspezifischen Allokationsroutinen kalibriert werden, damit die dynamische Partitionierung und Kohlenstoffeinträge durch tiefe Wurzeln genauer erfasst werden.

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Chapter 1

General Introduction

Agriculture is essential for global economies and food security, as it provides food and resources, and serves as a primary income source for billions of people. However, the current production systems have led to increased environmental damage, including resource depletion, soil degradation, and loss of biodiversity, threatening long-term food security and ecosystem health (Ullah and Shabir, 2023; Bulut and Gökalp, 2022). To address these issues, agriculture must become more sustainable, by producing enough food while protecting natural resources. One key challenge is the loss of soil fertility in essential minerals, which reduces crop yields and food quality, negatively impacting the health and nutrition of communities that depend on agriculture (Basiry et al., 2024). At the same time, water resources are becoming limited, further increasing the risk of yield losses (Forouzani and Karami, 2010). Soil degradation caused by erosion, compaction, and salinization reduces soil quality, cause additional challenges for crop management, increasing the risk of food shortages (Verma et al., 2015; Steenkamp et al., 2021).

Climate change in the future is expected to put additional pressure into crop production. Higher temperatures, elevated CO_2 levels, shifting rainfall patterns, and more frequent extreme weather events are disrupting crop growth and the balance between plants and soil (Maffia et al., 2023). These effects often interact with farming practices, particularly tillage. While tillage helps control weeds and prepares the soil, repeated use can damage soil structure, increase erosion, and reduce soil organic carbon levels (Polidoro et al., 2021; McCauley and Barlow, 2023). The loss of soil carbon not only affects fertility but also limits the role of soils in climate mitigation.

A better understanding of how roots coordinate with shoots to manage resources and cope with some of the stresses described above, is key to improving crop efficiency and resilience. Roots are often the overlooked part of plant systems as they grow below ground, however they provide physical support, absorb water and nutrients, and help plants respond to environmental stress (Gregory et al., 2013; Houde et al., 2020). Roots have different responses to environmental conditions such as nutrient deficiencies, drought, elevated CO_2, and temperature. These factors shape root development and influence overall plant performance, especially in the context of climate change (Olšovská et al., 2024; Polidoro et al., 2021; Dasgupta and Mahanty, 2024).

Much of what is known about roots comes from studies in greenhouses or controlled environments. However, these do not fully reflect what occurs in the field, as soil characteristics vary, as well as other interactions with microbial communities and neighboring crops. Field studies provide more realistic insights into root behavior but come with technical and logistical challenges. Long-term experiments and multi-year data can help identify broader patterns and improve our understanding of root systems under real-world conditions (Rowe et al., 2016).

To translate empirical knowledge from field studies into decisions at farm and policy scales, researchers rely on process-based crop simulation models such as AgroC, MONICA, STICS and the modular framework SIMPLACE (Huang et al., 2009; Nendel et al., 2011; Brisson et al., 2003; Enders et al., 2023). These models allow systematic exploration of genotype × environment × management (G × E × M) interactions, support climate-risk assessments and help optimise sowing dates, fertiliser rates and irrigation schedules (Wallach et al., 2018). Their capacity to run thousands of virtual scenarios makes them a practical complement to costly multi-site or long-term experiments.

Many current models, however, still represent the root system with coarse assumptions; typically prescribing a fixed maximum depth, simple uptake functions, and an oversimplified or static link to the shoot in the form of a constant root-to-shoot ratio (R/S). They also omit or simplify dynamic traits such as architectural plasticity, hydraulic redistribution, rhizodeposition, and root–microbe interactions (Dunbabin et al., 2013; Lobet et al., 2015; York et al., 2015). Strengthening these components with field-validated data is a critical step toward more accurate yield and resource-use forecasts and, ultimately, toward better planning for resilient and sustainable agriculture.

1.1 Root systems

Roots anchor plants, absorb water and nutrients, store carbohydrates, and mediate below-ground signalling, making them central to crop productivity and stress resilience (Bellini et al., 2014; Leitner et al., 2010; Zhu et al., 2006). Beyond supporting the shoot, they shape the soil itself: growing roots create pores that improve aeration and water retention, release organic compounds that sustain rhizosphere microbes, and form symbioses such as mycorrhizae that boost phosphorus acquisition (Freschet et al., 2021b; Fitzpatrick et al., 2018; Xiao et al., 2023; Hassan et al., 2019). Through these processes, root systems influence both plant nutrition and overall soil quality.

The efficiency of these functions depends on root system architecture; traits such as depth, growth angle, branching density, diameter and surface area. For example, primary axes provide anchorage and deep water access, whereas fine laterals and root hairs enlarge the absorbing surface (Bellini et al., 2014; Zhu et al., 2006). Physiologically, roots synthesise and transport hormones (e.g. auxin, ethylene) that adjust architecture in response to drought or nutrient scarcity and release exudates that modify soil pH and microbial activity (Choudhary et al., 2021; Lynch, 2021; Hassan et al., 2019).

The structural and functional characteristics of root systems are largely influenced by genetic traits, which determine their structure and behavior, including responses to environmental conditions. Quantitative-trait-locus mapping and genome-wide association studies indicate that traits such as root angle, branching density and hair length are typically polygenic, with additive and epistatic effects distributed across the genome (Hochholdinger and Tuberosa, 2009; Topp et al., 2013). Yet single genes of large effect can markedly shift architecture: *DEEPER ROOTING 1* (DRO1) and *PHOSPHORUS STARVATION TOLERANCE 1* (PSTOL1) in rice (*Oryza sativa*) promote steeper growth angles and faster early root development, respectively, improving performance on dry or P-deficient soils (Uga et al., 2013; Mai et al., 2014). In wheat (*Triticum aestivum*), specific alleles are linked to deeper rooting under drought (Hendel et al., 2021; Hamada et al., 2011), while transcription factors such as *ROOTLESS CONCERNING CROWN AND SEMINAL ROOTS*

(RTCS) in maize (*Zea mays*) integrate hormone signals that determine seminal and crown-root initiation (Hochholdinger et al., 2018).

These genetic controls operate in relation with environmental drivers. Early root vigour in maize, for example, is a reliable predictor of subsequent root development under field conditions (Jiang et al., 2018). Functional "phenes" such as dense, long root hairs directly enhance phosphorus uptake in low-P soils, and when combined with mycorrhizal associations or organic-acid exudation they form integrated strategies for P acquisition (Figure 1.1) (Lynch and Brown, 2008). Similar genotype-specific responses are observed in peanuts under water stress (Carrega et al., 2019) and in wheat subject to varying tillage regimes (Polidoro et al., 2021). Understanding how genetic variation interacts with management and environment to shape these phenes is therefore critical for breeding crops with more efficient and climate-resilient root systems.

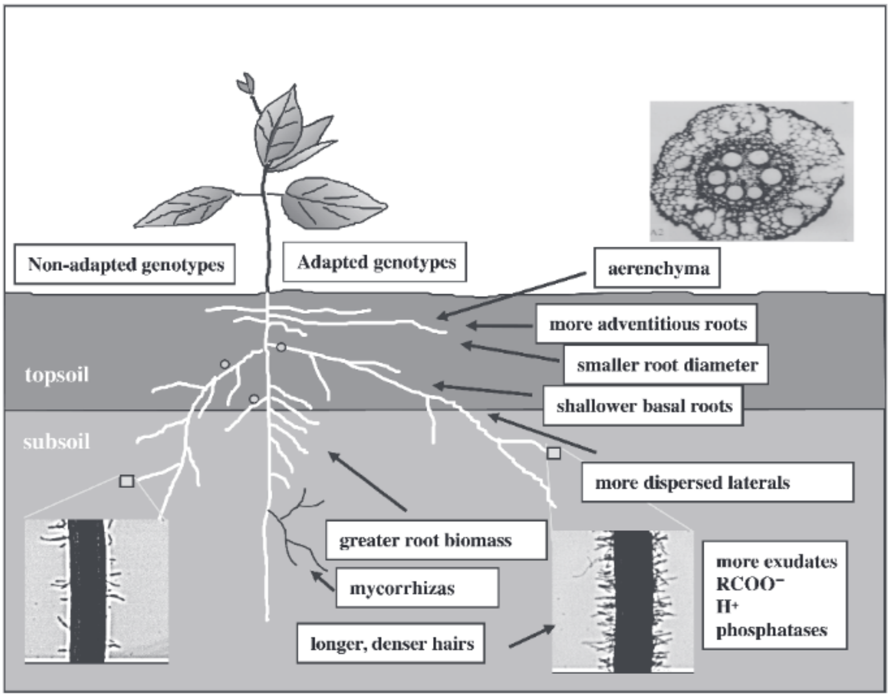

Figure 1.1: Changes in root architecture, morphology, and anatomy associated with adaptation to low P in common bean (Lynch and Brown, 2008).

1.2 Root systems classification

Root systems vary widely in their form and function. Table 1.1 summarizes the main ways to classify roots: by morphology, anatomical origin, developmental timing, and functional role.

Table 1.1: Classification types of roots according to morphology, anatomy, development, and function.

Classification type	**Sub-types**	**Key distinguishing features**	**References**
Morphology (Fig. 1.2)	Taproot	One thick primary root that grows vertically, penetrates deep horizons, laterals emerge along its length; efficient for accessing sub-soil water and anchoring the plant. For example carrots.	Tang et al. (2011)
	Fibrous	Many slender roots that originate near the stem base, form a dense, highly branched network in the topsoil; large surface area for rapid uptake of shallow water and nutrients. For example maize.	Tang et al. (2011)
Anatomy / origin (Fig. 1.3)	Adventitious	Roots arise post-embryonically from stems, hypocotyls, or leaves; often induced by flooding, wounding, or mechanical stress; add support and improve aeration.	Kawasaki et al. (2018)
	Seminal	First roots produced by the embryo (radicle and early laterals); establish early water and nutrient supply before shoot emergence; may later be replaced by adventitious roots.	Tang et al. (2011)
Developmental timing	Primary	Initial root axis derived from the radicle; indeterminate growth, forms the structural backbone of the system.	Smith and De Smet (2012)
	Secondary	Laterals that branch from primary or adventitious roots; multiply root tips and exploit additional soil volumes.	Smith and De Smet (2012); Morris et al. (2017)
Function	Anchoring	Thickened structural roots that stabilize the plant and resist lodging or uprooting.	Petricka et al. (2012)
	Foraging	Fine, highly branched roots with high surface-to-volume ratio; explore new soil zones for water and nutrients; short lifespan.	Petricka et al. (2012)
	Storage	Swollen roots that accumulate carbohydrates or other reserves, enabling regrowth and stress survival.	Rusyn et al. (2023)
	Symbiotic	Roots modified (e.g., mycorrhizal, modulated) to host microbial partners that enhance nutrient acquisition and stress tolerance.	Üstüner et al. (2022)

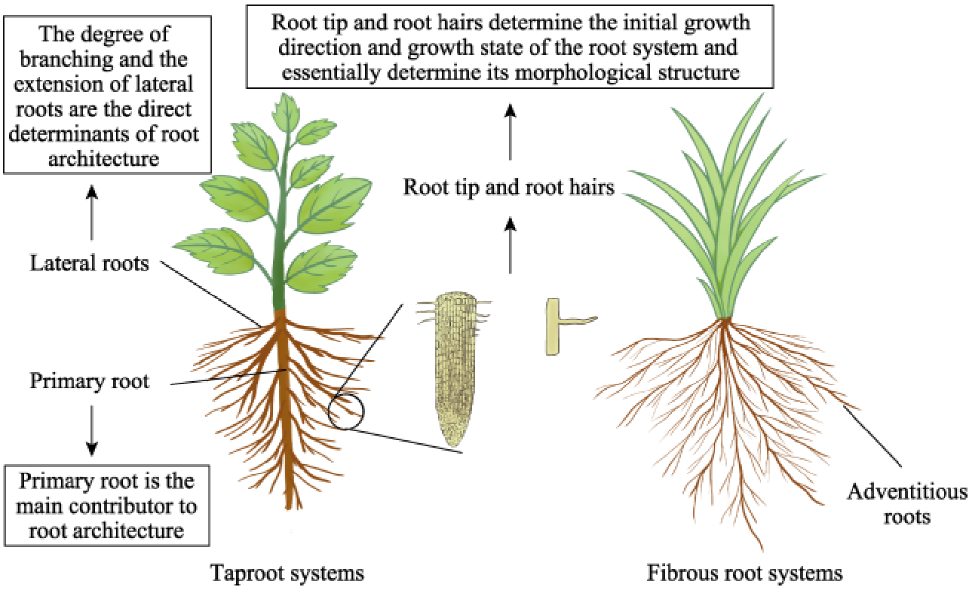

Figure 1.2: Type of roots according to morphology classification. Source: Zhiyong et al. (2023).

1.3 Root and Shoot Coordination

The root and shoot interconnectedness in plants is crucial for overall plant health, growth, and resource allocation (Shabala et al., 2016; Lucas et al., 2013). This relationship is characterized by complex signaling pathways, nutrient and water transport mechanisms, and growth regulatory interactions that ensure plants respond appropriately to environmental conditions. Root-to-shoot and shoot-to-root communication is facilitated by the transport of various signaling molecules, including hormones and peptides. For instance, the expression of specific peptides from the shoot regulate certain root functions, such as nitrate uptake (Ota et al., 2020). A hydraulic signal is also transmitted from roots to shoots to communicate water availability, which prompts stomatal regulation and thus affects photosynthesis (Christmann et al., 2007). This reciprocal communication affects growth and metabolic regulation, enabling plants to adapt to fluctuating nutrient availability and hydric stress. Additionally, abscisic acid, synthesized in roots, plays a significant role in managing shoot responses to water stress and nutrient status (Thompson et al., 2006).

On the other hand, the xylem transports water and nutrients from roots to shoots, enabling photosynthesis in leaves (Xu et al., 2009). This process depends on root structure and mycorrhizal associations that boost nutrient uptake (Chen et al., 2020b). In turn, shoots influence root growth by directing resources based on their development and nutrient needs (Chen et al., 2020a). The interactions between root and shoot systems become even more pronounced under environmental stress, such as drought or nutrient deficiency. Adjustments in root morphology, such as increased root length and density, can occur as a response to signals coming from the shoot, indicating physiological needs (Junior et al., 2017; Zhang et al., 2015).

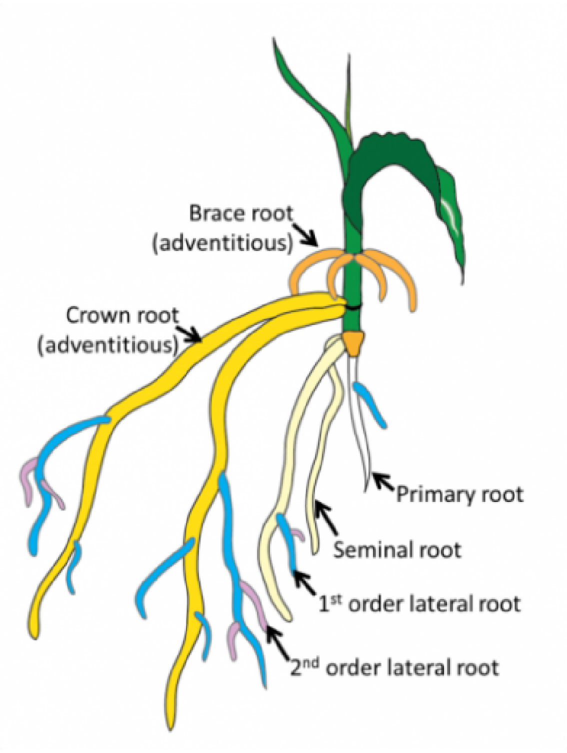

Figure 1.3: Example of anatomical classification of roots. Source: Steffens and Rasmussen (2016).

Roots can also alter their architecture to optimize foraging for water and nutrients when shoots signal their need. Conversely, a stressed root system can downregulate shoot growth to conserve energy and resources (Robbins and Pharr, 1988).

Hormone growth regulators between the root and shoot systems ensure that physiological processes are synchronized. Cytokinins transported from roots to shoots promote shoot growth, while auxins produced in the shoot can influence root elongation and branching (Yanthan et al., 2017). Thus, the balance between root and shoot growth is pivotal, especially in competitive environments where resource allocation may determine plant success (Lamb et al., 2008).

1.4 Environmental Factors Affecting Root and Shoot Development

Root systems exhibit considerable plasticity in response to soil heterogeneity and environmental factors (Schneider and Lynch, 2020; Lynch, 1995). This adaptive flexibility allows plants to modify root architecture to optimize resource acquisition under varying conditions. Hormonal signaling, particularly involving auxins, plays a key role in regulating this plasticity by influencing root branching and elongation patterns (Malamy, 2005; Rowe et al., 2016; Qin and Huang, 2018). The following sections describe how different environmental factors shape root architecture and their relation with the shoot.

1.4.1 Soil Nutrient Deficiencies

Nutrient deficiencies cause significant changes in root morphology, architecture, and physiology, often as adaptive strategies to improve nutrient acquisition. When nutrients such as nitrogen (N), phosphorus (P), or potassium (K) are limited, plants commonly increase their R/S, reallocating more biomass to root systems to explore a larger soil volume (Liang et al., 2022; Cabeza and Claassen, 2017; Wang et al., 2024b). For example, in *Arabidopsis thaliana*, nutrient stress often triggers increased lateral root formation and fine root development to improve nutrient absorption efficiency (Forieri et al., 2016; Gruber et al., 2013; Gahoonia et al., 2007; Becquer et al., 2021).

Gruber et al. (2013) found that moderate N deficiency increased total root length by 48%, with stronger N limitation leading to a higher R/S due to relatively less reduction in root biomass. N deficiency was also associated with longer lateral roots and stimulated root hair formation in crops like spinach, tomato, and rape (Foehse and Jungk, 1983). In split-root systems, root hair development was only observed when part of the root system had access to N-rich media.

Under P deficiency, plants often invest in shallower, horizontally spreading root systems that concentrate growth in topsoil layers where P is more available (Lynch and Brown, 2001; Rogers and Benfey, 2015; Bonser et al., 1996). Mechanisms such as organic acid and carboxylate secretion help mobilize P from bound forms (Hodge et al., 2009), while root hairs increase both in length and number to enhance surface area for uptake (Schmidt, 2001; Lambers et al., 2006). Denser root hairs and specific root traits, in combination with symbiotic mycorrhizal associations, play critical roles in nutrient uptake under low-P conditions (Kumar et al., 2019; Brundrett, 2002).

In contrast, research on root responses to K deficiency remains limited, though studies show a substantial reduction in primary root length and root biomass in *Arabidopsis*, while the R/S remained stable (Gruber et al., 2013).

Nutrient stress triggers physiological and metabolic changes, often reducing shoot growth and redirecting photosynthates to roots (Chea et al., 2021). However, lower shoot photosynthesis reduces carbohydrate availability for root growth, especially under nitrate and phosphate deficiencies (Song et al., 2019; Esfahani et al., 2022). These combined effects reduce biomass and crop yields, highlighting the need for balanced root–shoot allocation under stress (Wang et al., 2024b).

1.4.2 Tillage

Appropriate tillage practices can contribute to maintaining favorable soil conditions for root penetration. Tillage methods (classified broadly as conventional, conservation, or no-tillage) strongly affect soil conditions, crop yields, and farm management. Each method has specific benefits and drawbacks (Orzech et al., 2021; Handiso et al., 2023; Álvaro Fuentes et al., 2007).

Conventional tillage typically involves multiple passes of mechanical equipment, mixing and aerating the soil in ways that help break down organic matter, improve seedbed preparation, and enhance water infiltration during early growth. However, it can ultimately lead to compaction and reduced soil health over time (Orzech et al., 2021; Handiso et al., 2023; Álvaro Fuentes et al., 2007). Although conventional tillage may initially increase soil porosity, long-term use has been associated with soil erosion and a loss of soil organic matter (Handiso et al., 2023; Álvaro Fuentes et al., 2007). Regarding roots, conventional tillage can initially improve root penetration by decreasing soil compaction (Ji et al., 2013), thereby increasing the depth from which roots can access water and nutrients (Ji et al., 2013). Overall, conventional tillage tends to lower the R/S compared to conservation practices, since it promotes shoot growth more than root extension (You et al., 2017). Deep tillage, also considered part of conventional tillage, physically disrupts soil layers to a greater depth to alleviate compaction (Ruis et al., 2021), aiding deep rooting and better aeration (Ji et al., 2013; Piao et al., 2019). Nonetheless, it may elevate the risk of erosion. Schneider et al. (2017) note that deep tillage may improve yields by loosening soil compaction, though success depends on specific soil characteristics and the exact depth of tillage.

Conservation tillage encompasses practices such as strip-tillage and reduced tillage, which leave at least 30% of crop residues on the soil surface (Čopec et al., 2015). These methods help preserve soil structure and water retention while reducing erosion. Some research has found that conservation tillage systems can raise yields in certain situations and increase soil capacity for holding water and nutrients more effectively than conventional systems (Čopec et al., 2015; Kováč et al., 2005; Alam et al., 2014). Conservation practices also often promote higher soil organic matter (González et al., 2022). Consequently, these practices have gained attention as a way to sustain productivity while mitigating environmental harm. Ultimately, conservation practices can enhance root biomass and promote deeper root systems (Tumisang et al., 2021; Zheng et al., 2023).

No-tillage represents a form of conservation tillage whereby the soil is left entirely undisturbed prior to sowing, preserving natural structure and helping retain moisture. This method can increase soil organic carbon (González et al., 2022; Alam et al., 2014), although it may temporarily limit certain nutrients. In terms of belowground traits, no-tillage systems often increase root depth and density by preserving soil moisture and reducing compaction (Plaza-Bonilla et al., 2014; Wu et al., 2020). This deeper rooting can help synchronize roots with nutrient-rich zones (Kaur et al., 2023; Yeboah et al., 2017). No-tillage generally promotes a higher R/S than conventional tillage—plants often form deeper roots with greater biomass (Anugroho and Kitou, 2020).

1.4.3 Drought

Drought stress triggers significant morphological, physiological, and hormonal changes in plant root systems. Common adaptations include the increase in R/S (Dien et al., 2017; Mwenye et al., 2019), and the development of deeper and more extensive roots to enhance water uptake from subsoil layers (Beyaz, 2022; Dien et al., 2017; Studer et al., 2017). This includes increased root length, diameter, and xylem development, all of which improve the plant's capacity to access moisture under water-limited conditions (Kadam et al., 2015; Tracy et al., 2020). These structural changes are regulated by physiological signals, particularly the hormone abscisic acid, which promotes root growth and restricts shoot expansion under water stress (KHAN et al., 2023; Fenta et al., 2014). Drought also affects the balance of other hormones, modulating root and shoot development dynamically (Niu et al., 2008; Ruttanaprasert et al., 2015). Drought responses vary across plant species and genotypes (Zhou et al., 2018). Drought-tolerant varieties tend to exhibit stronger root growth responses, with higher R/Ss that improve resource acquisition and resilience (Jones et al., 2022).

1.4.4 Atmospheric CO_2 and Air Temperature

Elevated CO_2 modifies root morphology by promoting more extensive fine roots and branching (Nie et al., 2013; Iversen, 2009), enhancing plasticity and allowing plants to exploit resources more efficiently, often resulting in an increased R/S (Montealegre et al., 2000; Varga et al., 2022). Additionally, increased CO_2 can alter root exudation patterns, influencing soil microbes and creating a feedback loop that further stimulates root development (Graaff et al., 2006; Rosado-Porto et al., 2021; Gavito et al., 2001). Enhanced water-use efficiency under elevated CO_2 also favors root expansion in drier conditions, helping plants withstand drought stress by allocating more biomass belowground (Cha et al., 2017; Williams et al., 2018; Pregitzer et al., 2000).

Temperature plays a similarly pivotal role in shaping root and shoot allocation. In cooler soils, plants may channel more biomass to roots—partly because root growth is less restricted than shoot growth at lower temperatures—thereby increasing the R/S and maintaining resource uptake (Luo et al., 2013; Sakamoto and Suzuki, 2015a,b; Reich et al., 2014). By contrast, high temperatures initially boost metabolic activity but can damage roots over time, restricting their biomass and impairing nutrient absorption (Virjamo et al., 2014; Su et al., 2024).

1.5 Bridging Theory with Field Experiments

Research on plant roots can be conducted at different scales, including controlled environments (such as seedling, pot experiments, and greenhouses) and field experiments. Each of these environments presents advantages and challenges (Table 1.2), which can influence the outcomes of studies on root morphology, development, and the R/S.

Table 1.2: Scales for roots investigation.

Approach	**Conditions**	**Advantages**	**Disadvantages**	**Representative methods**	**References**
Laboratory methods	Highly controlled	Real-time imaging of root growth, non-destructive sampling, precisely controlled treatments, high repeatability, minimal space requirements, easy root clean-up.	Container walls modify root-system architecture (RSA), sterile media exclude beneficial microbes, results may lack field relevance.	Rhizophonics (nylon-fabric rhizotron in nutrient solution, 2-D imaging), Rhizoslides (plexiglass cassette with moist paper for early-stage imaging).	Paez et al. (2015)
Greenhouse methods	Moderately controlled	Intermediate realism between lab and field, control over soil type, moisture, light, temperature, pot size, and nutrient inputs, allows genetic assessment of RSA without intraspecific competition.	Labor-intensive handling of larger root systems, potential for disease/insect pressure, container still influences RSA, absence of soil biota and neighboring-plant effects unless added.	X-ray CT / MRI (3-D reconstruction of intact soil cores), Rhizotron / glass-wall box (continuous monitoring through transparent panel).	Paez et al. (2015); Schulz et al. (2013); Prieto et al. (2011)
Field methods	Minimally controlled	High physiological and agronomic relevance.	Labor- and time-intensive, high spatio-temporal variability in soil and climate, destructive or semi-destructive sampling, high cost depending on technology, specialized know-how needed.	Shovelomics (crown excavation and scoring), Profile wall / trench (vertical pit mapping), Soil coring / core-break (biomass and length density), Minirhizotron tubes (repeated in-situ imaging), Ground-penetrating radar (3-D mapping of coarse roots), Electrical resistivity/capacitance sensing (bulk root activity proxy), Spectral electrical impedance tomography (sEIT; frequency-dependent biomass imaging).	Paez et al. (2015); Tracy et al. (2020); Michels et al. (2024); Tsang et al. (2023); Fenta et al. (2014); York et al. (2015); Rongsawat et al. (2021); Iijima and Matsushita (2011); Lärm et al. (2024)

Despite the reproducibility and mechanistic insight offered by controlled systems, root studies in the field remain essential because they expose plants to the full spectrum of spatially and temporally variable stimuli that govern water and nutrient capture. Heterogeneous soil structure, fluctuating moisture, dynamic microbiomes, and inter-plant competition collectively shape root architecture and carbon allocation in ways that are seldom reproduced in pots or growth chambers (Füllner et al., 2011; Nagel et al., 2012; Aguilar et al., 2020). Field-based phenotyping therefore provides the trait–environment context needed to identify genotypes with robust performance under production conditions and to calibrate crop-growth models that underpin agronomic recommendations and climate-resilience assessments (Bucksch et al., 2014; Kalra et al., 2023).

Field work also introduces practical constraints. Soil heterogeneity complicates sampling; destructive methods such as coring or excavation may under-represent deep or fragile roots; and non-destructive tools (including minirhizotrons, spectral electrical impedance tomography, and ground-penetrating radar) balance resolution, cost, and throughput (Tsang et al., 2023; Fenta et al., 2014; Michels et al., 2024). Recent advances in imaging, automated analysis, and sensor networks now allow direct quantification of traits such as depth distribution, rhizosphere activity, and genotype × environment interactions at operational scales (Prieto et al., 2011; **?**; Holz et al., 2024). These developments strengthen the link between controlled studies and field performance and support the wider use of root phenotyping in crop improvement programs.

1.6 Representation of Roots and Carbon Inputs in Process-Based Soil-Crop Models

Simulation models translate physiological understanding of crops and soils into quantitative tools for scenario analysis. At field scale, process-based models combine sub-modules for micro-meteorology, soil water and N dynamics, root and shoot growth, residue turnover and soil-organic-carbon (SOC) decomposition, thereby linking short-term management decisions with long-term carbon-sequestration outcomes (Jacobs et al., 2020; Keel et al., 2017). Model applications now range from estimating SOC changes for greenhouse-gas reporting to testing climate-risk mitigation strategies (Riggers et al., 2021). Uncertainty nevertheless arises from the way individual models represent plant carbon inputs, particularly the partitioning between shoot, root and exudate pathways (Wallach et al., 2024).

Four widely used, open-source platforms exemplify both the capabilities and current gaps:

- **MONICA**: a modular model emphasising coupled carbon-nitrogen cycling; recent optimisation has improved its SOC turnover routine and yield predictions across European sites (Nendel et al., 2011; Farina et al., 2021).
- **STICS**: a daily time-step model widely employed for crop-management optimisation; its latest JavaSTICS 10.2 release adds enhanced phenology options and updated cultivar parameters (Brisson et al., 2003).

- **AgroC**: originally developed for carbon budgeting, now extended with explicit routines for root exudation and microbial use of labile C, making it one of the few frameworks able to simulate this input pathway (Huang et al., 2009; Klosterhalfen et al., 2017).
- **SIMPLACE**: a flexible “wrapper” that couples interchangeable component models, allowing users to tailor complexity from simple “light-water-nitrogen” runs to full ecosystem carbon balances (Enders et al., 2023).

All four models calculate root biomass from shoot assimilation using empirical allocation rules. Most still apply fixed maximum rooting depths and constant R/Ss, oversimplifying drought- or nutrient-induced plasticity and ignoring feedbacks between root development, soil structure and SOC formation (Couëdel et al., 2024). Only AgroC currently represents rhizodeposition explicitly; none resolve hydraulic redistribution or root–microbe interactions. Validating these process descriptions in field experiments is essential for reducing uncertainty in projections of crop yield, soil-organic-carbon sequestration, and greenhouse-gas balances under increasingly frequent heat, drought, and excess-water events (Kim et al., 2024; Webber et al., 2022; Peng et al., 2020).

1.7 General Objective and Research Questions

General Objective

This thesis aims to quantify how nutrient deficiencies influence root traits and to determine how nutrient stress, tillage practices, and emerging climate pressures (drought, warming and elevated CO_2) reshape root-to-shoot biomass partitioning in arable crops at field scale. A further objective is to evaluate how accurately four process-based soil–crop models reproduce these field-observed responses in R/Ss and evaluate their sensitivity in a scenario analysis.

Research Questions

To meet the general objective, the work is structured around four specific research questions, each addressed in a separate chapter:

1. What is the magnitude and direction of the changes in root length, root biomass, specific root length and the R/S that occur when N, P or K are deficient under field conditions across major arable crops? (chapter 2).
2. In a long-term field experiment, how does the sustained omission of N, P, K or lime alter seasonal winter-wheat root development and root-to-shoot allocation? (chapter 3).
3. Across contrasting climates and soils, under what circumstances (and by how much) does switching between conservation/no-till and conventional tillage modify the R/S of field crops? (chapter 4).

4. How do the models MONICA, STICS, AgroC and SIMPLACE differ in their sensitivity to nutrient deficiency, tillage, drought, elevated CO_2 and warming when simulating root biomass, root-to-shoot partitioning and soil-carbon inputs, and which specific process formulations drive those differences? (chapter 5).

Chapter 2

Nutrient deficiency effects on root architecture and root-to-shoot ratio in arable crops

This chapter has been published as:
Lopez, G., Ahmadi, S. H., Amelung, W., Athmann, M., Ewert, F., Gaiser, T., Gocke, M. I., Kautz, T., Postma, J., Rachmilevitch, S., Schaaf, G., Schnepf, A., Stoschus, A., Watt, M., Yu, P., & Seidel, S. J. (2023). Nutrient deficiency effects on root architecture and root-to-shoot ratio in arable crops. *Frontiers in Plant Science*, 13. `https://doi.org/10.3389/fpls.2022.1067498`

Abstract

Plant root traits play a crucial role in resource acquisition and crop performance when soil nutrient availability is low. However, the respective trait responses are complex, particularly at the field scale, and poorly understood due to difficulties in root phenotyping monitoring, inaccurate sampling, and environmental conditions. Here, we conducted a systematic review and meta-analysis of 50 field studies to identify the effects of nitrogen (N), phosphorous (P), or potassium (K) deficiencies on the root systems of common crops. Root length and biomass were generally reduced, while root length per shoot biomass was enhanced under N and P deficiency. Root length decreased by 9% under N deficiency and by 14% under P deficiency, while root biomass was reduced by 7% in N-deficient and by 25% in P-deficient soils. Root length per shoot biomass increased by 33% in N deficient and 51% in P deficient soils. The root-to-shoot ratio was often enhanced (44%) under N-poor conditions, but no consistent response of the root-to-shoot ratio to P-deficiency was found. Only a few K-deficiency studies suited our approach and, in those cases, no differences in morphological traits were reported. We encountered the following drawbacks when performing this analysis: limited number of root traits investigated at field scale, differences in the timing and severity of nutrient deficiencies, missing data (e.g., soil nutrient status and time of stress), and the impact of other conditions in the field. Nevertheless, our analysis indicates that, in general, nutrient deficiencies increased the root-length-to-shoot-biomass ratios of crops, with impacts decreasing in the order deficient P> deficient N> deficient K. Our review resolved inconsistencies that were often found in the individual field experiments, and led to a better understanding of the physiological mechanisms underlying root plasticity in fields with low nutrient availability.

2.1 Introduction

Sustainable intensification of agriculture is one promising way to meet the expected global increase in demand for food, fiber, fodder, and biofuel (Godfray and Garnett, 2014). However, edaphic stresses such as drought, soil nutrient availability, high acidity, and high salinity severely limit worldwide production. Managing nutrient deficiencies may be difficult, considering that the global efficiency of fertilizer application is frequently not more than 50% for nitrogen (N), less than 10% for phosphorus (P), and about 40% for potassium (K) (Fageria, 2012). Excessive fertilization may, in turn, promote groundwater pollution and gaseous N emissions. Hereby, the European Commission targets a 20% reduction in fertilizer quantities and a 50% reduction in nutrient losses by 2030 (Commission, 2020).

Studies focusing on roots and on their role in nutrient acquisition are crucial to lay the basis of management strategies to increase crop production while improving resource use efficiency (Gregory et al., 2013). Root systems are strongly influenced by a wide range of abiotic factors such as gravity, soil compactness, soil water content, soil texture, aeration, nutrient availability, pH, and temperature (Yapa et al., 1988; Bengough et al., 2011; Kopke et al., 2015; Schneider et al., 2017; Hartmann et al., 2018; Correa et al., 2019; Hadir et al., 2021). Biotic factors (e.g., bacteria, fungi, nematodes, etc.) can also affect biogeochemical processes and affect the root morphology in the soil (Larsen et al., 2015). And vice versa, the root exudates stimulate microbial flora activity by fostering enzyme production. The microorganism decompose the soil organic matter, and consequently, the amounts of nutrients (N, P) increase, affecting the morphological traits in roots (Barrios-Masias et al., 2019).

Root systems can exhibit a high degree of plasticity in response to physical, chemical and biological changes in the environment (Lynch, 1995; Ostonen et al., 2007; Rich and Watt, 2013; Correa et al., 2019). For example, as reviewed by Correa et al. (2019), roots showed a retarded development as sign of apparent plasticity[1]., including changes in architecture, as a response to severe stress (e.g. soil compaction). These architectural changes may in turn enhance the tolerance to variations in the environmental conditions (adaptive plasticity). Drew et al. (1973) showed that plants grown on nutrient-rich soil patches increased number and length of fine lateral roots, thus positively affecting the overall specific root length (SRL).

Gruber et al. (2013) grew Arabidopsis plants on agar at four deficiency levels for 12 nutrients and quantified seven root traits. Total root length increased by 48% under moderate N deficiency and decreased under most severe N deficiency. Furthermore, since the root biomass decreased comparatively less than the shoot, the root-to-shoot ratio gradually increased with decreasing N supply. In addition, N deficiency stimulated the growth of a more exploratory root system with long lateral roots.Foehse and Jungk (1983) reported that some N deficiency level stimulates root hair formation of spinach, tomato, and rape in pot experiments. Additionally, plants grown at low N displayed longer root hairs than plants grown at higher N concentrations. Moreover, when oilseed rape was grown in a split-pot system, root hairs did not form when all root system grown in media with poor N supply, whereas

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[1] Plasticity is defined as the reorganization of the root architecture in response to one or several external disturbances that affect and impact the root morphology (Correa et al., 2019)

root hairs were formed when at least part of the roots (10%) was grown in N-rich media.

Crops cope with P deficiency by increasing root development in the P-rich zone (commonly in the topsoil) (Lynch and Brown, 2001; Rogers and Benfey, 2015), releasing carboxylates that capture iron and aluminium from the respective phosphates, thus rendering P more soluble (Hodge et al., 2009), as well as directing arbuscular mycorrhizal uptake pathways (Smith et al., 2018)). Total root length generally decreases with P deficiency (Gruber et al., 2013; Haling et al., 2018), and the growth of primary and lateral roots is restrained when roots reach a low-P zone (Desnos, 2008). However, roots can also develop a shallower, horizontal, and highly branched root system (Lynch and Brown, 2001; Gruber et al., 2013; Müller et al., 2015). For example, beans develop more horizontal root angles under P-limited soil, resulting in a more extensive root area in the topsoil, where P was more concentrated than in the subsoil (Bonser et al., 1996). Another well-known mechanism to enhance the P acquisition in P-limited conditions is the increase in length and number of root hairs (Schmidt, 2001; Lambers et al., 2006).

In contrast to the numerous studies investigating root responses to N and P deficiencies, research on the effects of K deficiency in roots is scarcer. Notably, a study with Arabidopsis showed a decrease in root biomass (about 60%) and primary root length at the lowest supplied K concentration, while root-to-shoot ratios remained stable across different levels of K deficiency (Gruber et al., 2013).

The current understanding of root plasticity has been mostly derived from seedlings and pot experiments conducted in controlled environments such as greenhouses or phytochambers (López-Bucio et al., 2003; Rich and Watt, 2013). However, the root growth behaviors in those conditions are frequently different than those observed under field conditions due to several abiotic and biotic factors, which are more variable and differ significantly from those in the greenhouse (Rich and Watt, 2013; Watt et al., 2013; Heinze et al., 2016; Schittko et al., 2016; Rich et al., 2020). Plants growing in fields are usually grown in crop stands, thus interacting and competing with each other, changing their environment and that of their neighboring plants (Cahill et al., 2010; Faget et al., 2013; Weidlich et al., 2018). Thus, pot studies generally do not have the physical, chemical and microbial composition of field soils. This difference alters the growth rate and rooting depth of plants as compared to field studies (Eno and Popenoe, 1964; De Deyn et al., 2004; Passioura, 2006; Ruzicka et al., 2010, 2012; Poorter and Ryser, 2015; Howard et al., 2017). For instance, Mokany and Ash (2008) found a poor correlation of root biomass and root-to-shoot ratio in pot experiments vs. field conditions. Moreover, the root responses to any stress differ in pots compared to field, as shown in cassava, where the root weight and width were statistically similar under drought and irrigated conditions at field scale but different in the pot experiments (Kengkanna et al., 2019). Another limitation in pot studies is that the container shape affects root morphological characteristics. Roots of plants cultivated in smooth-sided containers can grow deformed or limit their growth because they cannot spread horizontally, as they would do in an open field, therefore, they expand vertically, wrapping up at the bottom of the pot (Amoroso et al., 2010; Oburger and Schmidt, 2016). Besides, the container influences the humidity, and ventilation of soil (Poorter et al., 2012).

Consequently, transferring observations on root morphology or plasticity from pot experiments to real field conditions is usually impossible.

To overcome these limitations, we performed a systemic review and meta-analysis to analyze whether and how N, P, and K deficiencies impact root morphological traits of common arable crops under field conditions. We were particularly interested in root length, root biomass, root diameter, root hair formation and root/shoot performance indices such as root-to-shoot ratio, root length per unit of shoot biomass and specific root length.

2.2 Materials and methods

We used a systematic review and meta-analysis approach to show the evidence of the effects of nutrient deficiencies on roots. The approach was as follows.

2.2.1 Data sources and search strategy

We used the electronic databases Web of Science, Google scholar, and Wiley online library to search for articles published in peer-reviewed journals without any restriction in the year of publishing. The exact combinations used for searching keywords was:

- Root + deficiencies + nutrients + field
- Root + nitrogen + field
- Root + nitrogen + site
- Root + phosphorus + field
- Root + phosphorus + site
- Root + potassium + field
- Root + potassium + site

In addition, secondary literature cited in selected papers was also looked up and included if relevant. In total, we considered 50 studies in which root growth of common field crops under field conditions was evaluated. All the key contents about the considered studies are summarized in the Tables A.1, A.2, A.3 of the Supplementary Material.

2.2.2 Selection criteria

The eligibility of the studies in this review was evaluated using the following criteria:

(i) Investigation of roots, with observed data of at least one of the following traits: root growth, root length, root biomass, root-to-shoot ratio and/or root hair formation.

(ii) Use of common agricultural crops.

(iii) Reduction (or deficiency) of at least one of the three macro-nutrients N, P, or K, including a non-fertilized/insufficient control treatment.

(iv) Experiments were conducted at a field-scale.

The exclusion criteria were:

(i) Only qualitative data available.

(ii) Forestry plants.

(iii) Small-scale (e.g., pot or bucket experiments) or laboratory experiments (e.g., plants grown on agar).

2.2.3 Observed root traits

The following root traits were considered:

(i) Root length and root length density (RLD)

(ii) Root biomass

(iii) Root mass density (RMD) or root weight density (RWD)

(iv) Root length per shoot biomass

(v) Root-to-shoot ratio

(vi) Specific root length (SRL)

(vii) Root diameter

(viii) Root hair formation

(ix) Speed of root growth

(x) Root surface area

For definitions, please refer to the glossary provided by Freschet et al. (2021a).

2.2.4 Data extraction

The extracted data for each study involved: i) name of the crop; ii) year of the study; iii) country of the experiment, iv) soil type; v) used method for root observation, vi) treatments; vii) effect on root morphology and distribution; and viii) effect on root length, root biomass, root diameter, shoot biomass and, root-to-shoot ratio, specific root length. Any other relevant information was also recorded and included in the text.

2.2.5 Estimation of the relative change of each trait due to nutrient deficiency

Besides an evaluation of the absolute trait values, the effect of the nutrient deficiency on each root trait was estimated using a relative change formula (Equation 1), where the value of the treatment without the specific nutrient was the comparison indicator.

$$Relative\ Change = \frac{X0 - X1}{X1} \tag{2.1}$$

Where X0 is the mean value of the trait (root length, biomass, etc.) without the nutrient application (e.g., 0 kg ha-1 of N) and X1 is the mean value of the trait with the nutrient addition (for example, application of 50 kg ha-1 of N). The relative change of root length, root biomass, root length per shoot biomass, root-to-shoot ratio, and diameter (if sufficient data was available) was calculated for each treatment and averaged for each study. Therefore, the mean of each study was considered as a single observation for the boxplots and the median estimation.

2.2.6 Statistical analysis

In order to compare the absolute values among the different studies, we normalized the absolute raw data with the following formula (Equation 2):

$$Normalized\ value\ x' = \frac{(x - X_{\min})}{(X_{\max} - X_{\min})} \tag{2.2}$$

Where x is the absolute value of the root trait (root length, biomass, etc.) with respect to a specific nutrient availability level, Xmin is the lower bound in the values' range (within the study and over all nutrient levels), and Xmax is the upper bound of the values' range.

Then, we averaged the normalized data (grouped by deficiency or non-deficiency) to have two single observations per study (deficient and non-deficient). A normalized value close to 0 or 1 indicates that the value is similar to the study's minimum or maximum values.

We then performed a t-test (t.test function of the stats R package) to compare the normalized data (one record per study if available) from deficient and non-deficient treatments and evaluate its statistical significance. The statistical analysis and all plots were created using the software R (version 4.0.2).

2.2.7 Considered studies

We found 32 studies that met the criteria of our search in the electronic databases and additional 18 publications cited within those studies. In total, 50 studies were analyzed in this work. We recognized that the keywords “field” and “site” were not often used in the titles or as keywords in our target studies, and thus additional papers were included through the references provided in the initially found manuscripts.

In the studies considered, the crops were grown in the USA, China, Australia, UK, Brazil, New Zealand, Iran, Costa Rica, Honduras, Canada, Mozambique, Colombia, Japan, Denmark, Germany and Belgium. Moreover, 29 out of 50 studies used fibrous root types (monocots) in their research, while the remaining 21 evaluated taproot root types (dicots). The studied crops are shown in Table 2.1.

2.3 Results

2.3.1 Relative change in root morphological traits under N, P, and K deficiency

Our meta-analysis revealed that root length and biomass, in most cases, decreased with increasing N, P, and K deficiency. Root length per shoot biomass and root-to-shoot ratio increased when plants were grown under N and P-deficient conditions. The specific root length was similar in nutrient-deficient and non-deficient treatments. The relative changes in root length, root biomass, root length per shoot biomass, root-to shoot ratio and specific root length under N, P and K deficiency are shown in Figure 2.1.

The magnitude (median) of the relative changes of the different root traits was similar among dicot and monocot plants under N and P deficiency (Supplementary Figure A.1). The relative change of root-to-shoot ratio was greater under P deficiency than P-added in monocots plants.

2.3.2 Nitrogen

The normalized root length, root biomass, root length per shoot biomass, and root-to-shoot ratio showed significant differences for N-deficient and non-deficient conditions (Figure 2.2). The normalized specific root length was similar in both treatments.

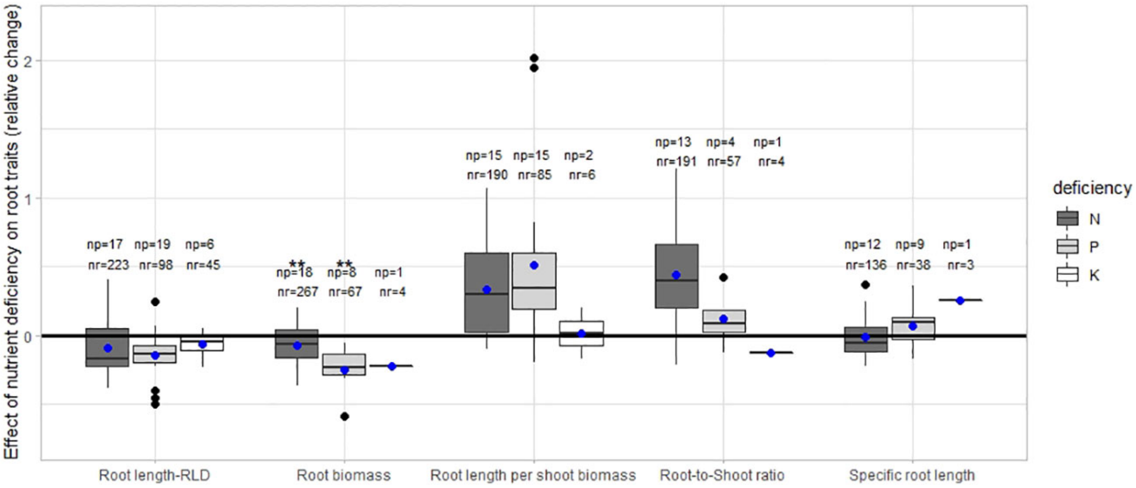

Figure 2.1: The relative change of the root traits under deficiency $\left(\frac{X0-X1}{X1}\right)$ where X_0 is the value in the treatment without any addition of the nutrient and X_1 is the value of the treatment with the nutrient application. *np* stands for the number of publications/studies considered in the calculation, and *nr* for the total number of observations within these publications. The line within the boxes refers to the median. ** stands for significant differences at a 0.95 confidence level. Blue dots represent the mean.

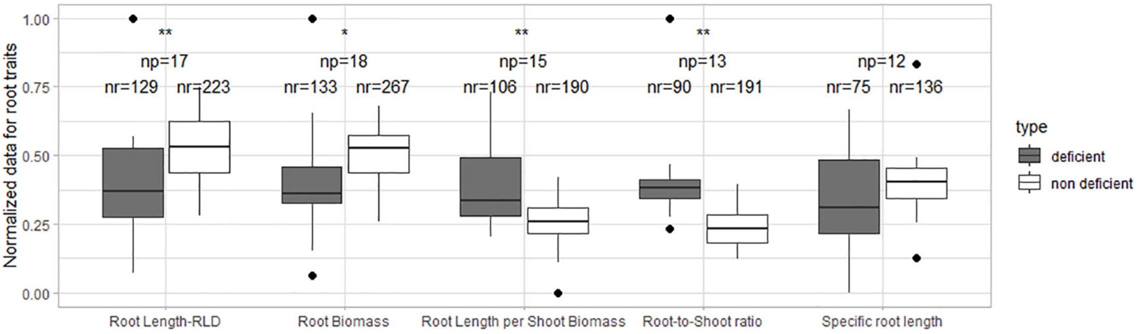

Figure 2.2: Boxplot of the normalized root data under N deficiency and N non-deficiency. A t-test was performed; * stands for significant differences at a 0.9 confidence level and ** at a 0.95 confidence level. *np* stands for the number of publications/studies considered in the calculation, and *nr* is the total number of observations within these publications.

Table 2.1: Number of studies per category at field-scale used for the systematic research.

Crop name (Latin name)		**Number of studies per crop**	**Nutrient deficiency**	**Number of studies per nutrient deficiency**
Barley	*Hordeum vulgare*	3	Nitrogen (N)	24
Common bean	*Phaseolus vulgaris*	7	Phosphorus (P)	19
Cotton	*Gossypium*	3	Potassium (K)	5
Maize	*Zea mays*	18	N and P	1
Millet	*Pennisetum glaucum*	1	N, P, and K	1
Oilseed rape	*Brassica napus*	2		
Potato	*Solanum tuberosum*	1		
Rice	*Oryza sativa*	1		
Sorghum	*Sorghum*	3		
Soybean	*Glycine max*	5		
Wheat	*Triticum aestivum*	6		
Sugarbeet	*Beta vulgaris*	1		
Sugarcane	*Saccharum officinarum*	1		
Buckwheat, castor, peanut, pigeon pea	*Fagopyrum esculentum, Ricinus communis, Arachis hypogaea, Cajanus cajan*	1		

Root length, root length density, and root surface area

Table 2.2 shows an overview of the studies that report the effects of N deficiency on the total root length or RLD. It also shows the crop, soil type, factors investigated in each study, and the overall impact. Most of the observations revealed that absolute root length and RLD were lower under conditions of N deficiency than under sufficient N supply, particularly at N0 [2] (Barber and Mackay, 1986; Anderson, 1987, 1988; Barraclough et al., 1989; Xue et al., 2014; Chen et al., 2020a; Hadir et al., 2021; Mehrabi et al., 2021; Fang et al., 2022). This was observed for maize (Anderson, 1988, 1987; Fang et al., 2022), winter wheat (Barraclough et al., 1989; Xue et al., 2014; Mehrabi et al., 2021), cotton and sugar beet (Chen et al., 2020a; Hadir et al., 2021).

Some studies reported variable effects on root length and RLD depending on the other studied factors. In this line, Mackay and Barber (1986); Sharifi et al. (2005) and Nakamura et al. (2002) reported a genotype effect of N deficiency on maize, potato and sorghum root morphology. Feng et al. (2016) and Comfort et al. (1988) observed a weak parabolic relationship between N supply and root length (in maize and spring wheat). Peng et al. (2012) outlined that the effect of N deficiency on maize root length was related to the crop's developmental stage. N deficiency (N0) stimulated root growth in early maize growth stages, and the total root length peaked before the tasseling, followed by an early decline compared with other treatments with increasing N supply in all three years studied.

In contrast, other studies found an increase in root length in N0 treatments. NaNagara et al. (1976); Thom and Watkin (1978) and Eghball and Maranville (1993) observed increased root lengths under zero N supply treatment compared with N-fertilized treatments of maize. Moreover, NaNagara et al. (1976) found that the effects of N fertilization on root length interacted with the tillage regime and development stage.

Root biomass

Table 2.3 summarizes the main effects of N deficiency on root biomass. Most of the observations show a decrease in the total root biomass in the N0 treatment, regardless the crop (Welbank and Williams, 1968; Myers, 1980; Barraclough et al., 1989; Nakamura et al., 2002; Sharifi et al., 2005; Otto et al., 2014; Xue et al., 2014; Schneider et al., 2017; Mehrabi et al., 2021; Fang et al., 2022), crop developmental stage (Myers, 1980; Barraclough et al., 1989; Nakamura et al., 2002; Sharifi et al., 2005; Xue et al., 2014; Welbank and Williams, 1968), genotype (Schneider et al., 2017; Fang et al., 2022), or irrigation regimens (Mehrabi et al., 2021).

Some studies found variable effects on root biomass depending on the other studied factors. Anderson (1987, 1988) reported that tillage treatments and year of cultivation affected maize root morphology differently under N deficiency. In the 3-year field experiment in three different soils types (loamy clay, clay loam, and sandy

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[2] Treatment description: N0 stands for no N fertilizer applied, N(N supply level) stands for the amount of N applied in kg ha^{-1} (e.g. N150: 150 kg N ha^{-1} were applied). This is similar for P and K nutrients (e.g. P0, P44, K0, K30).

Table 2.2: Studies that report effects of N deficiency on total root length and/or root length density (TRL-RLD) at field scale.

Reference	**Crop**	**Soil**	**Factors**	**TRL-RLD**
Chen et al., 2020	cotton	loamy	LEV	DECREASE
Anderson, 1987	maize	silty loam	DEV YEAR	DECREASE
Anderson, 1988	maize	silty loam	DEV YEAR	DECREASE
Fang et al., 2022	maize	loamy	LEV YEAR DEV	DECREASE
Hadir et al., 2021	sugar beet	silty loam	DEV	DECREASE
Barraclough et al., 1989	winter wheat	silty clay loam	IRR DEV	DECREASE
Mehrabi et al., 2021	winter wheat		PLAN IRR LEV	DECREASE
Xue et al., 2014	winter wheat		DEV LEV	DECREASE
Feng et al., 2016	maize	loamy clay, clay loam, sandy loam	SOIL YEAR LEV	VARIABLE
Mackay and Barber, 1986	maize	silty loam	GEN DEV	VARIABLE
Peng et al., 2012	maize	silty loam	DEV LEV YEAR	VARIABLE
Sharifi et al., 2005	potato		GEN DEV	VARIABLE
Nakamura et al., 2002	sorghum		GEN	VARIABLE
Comfort et al., 1988	spring wheat	silty loam, clay loam	GEN SITE LEV	VARIABLE
Eghball and Maranville, 1993	maize	silty clay loam	LEV	INCREASE
NaNagara et al., 1976	maize	silty loam	TILL DEV	INCREASE
Thom and Watkin, 1978	maize	sandy loam	DEV LEV	INCREASE

DECREASE (in red): diminished TRL-RLD, VARIABLE (in yellow): diverse, inconclusive, or no effects on TRL-RLD, and INCREASE (in green): large TRL-RLD in case of deficient vs. non-deficient conditions. Factors refer to the variables studied in each manuscript. LEV: several levels of N applied, DEV: several development stages investigated, YEAR: several years investigated, IRR: water treatments applied (such as irrigation and drought), PLAN: several planting methods tested, SOIL: several soil types tested, GEN: diverse genotype tested, SITE: different sites tested, TILL: several tillage practices tested. For more details refer to SI Table A.1.

Table 2.3: Studies that report effects of N deficiency on root biomass (RBIO) at field scale.

Reference	**Crop**	**Soil**	**Factors**	**RBIO**
Welbank and Williams, 1968	barley		DEV LEV	DECREASE
Fang et al., 2022	maize	loamy	LEV YEAR DEV	DECREASE
Schneider et al., 2017	maize	silt loam, clay loam	SOIL	DECREASE
Sharifi et al., 2005	potato		GEN DEV	DECREASE
Nakamura et al., 2002	sorghum		GEN DEV	DECREASE
Myers, 1980	sorghum	clay loamy	GEN DEV	DECREASE
Otto et al., 2014	sugarcane	Typic Kandiudox, Rhodic Eutrudox	SOIL LEV DEV	DECREASE
Barraclough et al., 1989	winter wheat	silty clay loam	IRR DEV	DECREASE
Mehrabi et al., 2021	winter wheat		PLAN IRR LEV	DECREASE
Xue et al., 2014	winter wheat		DEV LE	DECREASE
Chen et al., 2020	cotton	loamy	LEV	VARIABLE
Sainju et al., 2005	cotton	sandy loam	TILL LEV	VARIABLE
Anderson, 1987	maize	silty loam	DEV YEAR	VARIABLE
Anderson, 1988	maize	silty loam	DEV YEAR	VARIABLE
Feng et al., 2016	maize	loamy clay, clay loam, sandy loam	SOIL YEAR LEV	VARIABLE
Thom and Watkin, 1978	maize	sandy loam	DEV LEV	VARIABLE
Hadir et al., 2021	sugar beet	silty loam	DEV	VARIABLE
Wang et al., 2005	winter wheat	clay loam	IRR LEV YEAR	VARIABLE
Eghball and Maranville, 1993	maize	silty clay loam	LEV	INCREASE

DECREASE (in red): diminished RBIO, VARIABLE (in yellow): diverse, inconclusive or no effects on RBIO, and INCREASE (in green): higher RBIO in case of deficient as compared to non-deficient conditions. Factors refer to the variables studied in each manuscript. LEV: several levels of N applied, DEV: several development stages investigated, YEAR: several years investigated, IRR: water treatments applied (such as irrigation and drought), PLAN: several planting methods tested, SOIL: several soil types tested, GEN: diverse genotype tested, SITE: different sites tested, TILL: several tillage practices tested. For more details refer to SI Table A.1.

loam) conducted by Feng et al. (2016), less maize root biomass was found in N0 treatment, except in the loamy clay in one out of the three years. In another maize study, at early and grain-filling stages, plants grown under N0 conditions presented higher root dry weight than those submitted to N168 and N672 treatments (Thom and Watkin, 1978). In winter wheat, Wang et al. (2014) found that the effect of N on root weight density depended on soil water conditions. Root biomass under N deficiency reacted differently depending on the development stages (Hadir et al., 2021), level of deficiency (Chen et al., 2020a), and tillage (Sainju et al., 2005).

In contrast, only one study (Eghball and Maranville, 1993) reported increased maize root biomass under N deficiency and no interactions with the maize genotype. Dry maize root weight at N0 was higher than at N60, N120, and N180.

Root-to-shoot ratio

Table 2.4 describes the effects of N deficiency on two ratios: root-to-shoot and root length per shoot biomass, including the soil type and variables investigated in each study. Most of the studies reported an increase in the root-to-shoot ratio upon N deprivation (Welbank and Williams, 1968; Myers, 1980; Anderson, 1988; Eghball and Maranville, 1993; Sharifi et al., 2005; Wang et al., 2005; Farrior et al., 2013; Xue et al., 2014; Hadir et al., 2021), indicating a greater investment of assimilates into the belowground crop parts under low N conditions (Figure 2.2).

Two studies reported variable effects on the root-to-shoot ratio depending on the other studied factors. Feng et al. (2016) reported that the root-to-shoot ratio of maize at silking was higher in N0, except in the loamy clay soil in one out of the three years of the study. In sugarcane, N deficiency led to a decrease in root-to-shoot ratio at the beginning of the production cycle at one out of two experimental sites. In later growth stages, the root-to-shoot ratio was similar between the treatments (Otto et al., 2014).

Root diameter, root diameter distribution, and specific root length

All the studies that investigated the effect of N deficiency on root diameter and specific root length are listed in Table 2.5. Only a few studies reported observations of root radius, root diameter, root diameter distribution, or specific root length, and a predominant effect of N treatments on these traits cannot be identified. An increase in maize average root diameter in N0 as compared to N180 was observed in a long-term experiment (Anderson, 1987). In contrast, Sharifi et al. (2005) reported no effect of low N conditions on root diameter for potato. Otherwise, a decrease in average root diameter at N0 was reported for maize (Eghball and Maranville, 1993)and sugar beet experiment (Hadir et al., 2021).

Higher values of specific root length at N0 were found in maize (Anderson, 1987; Fang et al., 2022) and sorghum (Nakamura et al., 2002). In contrast, Mehrabi et al. (2021) reported a smaller SRL when N was not applied.

Table 2.4: Studies that report effects of N deficiency on the root-to-shoot ratio (R_S) and root length per shoot biomass (LENG_SHOOT) at the field scale.

Reference	**Crop**	**Soil**	**Factors**	**R_S**	**LENG_SHOOT**
Sharifi & Williams, 2005	potato		GEN DEV	INCREASE	INCREASE
Xue et al., 2014	winter wheat		DEV LEV	INCREASE	INCREASE
Eghball & Maranville, 1993	maize	silty clay loam	LEV	INCREASE	VARIABLE
Hadir et al., 2021	sugar beet	silty loam	DEV	INCREASE	DECREASE
Welbank & Williams, 1968	barley		DEV LEV	INCREASE	
Anderson, 1988	maize	silty loam	DEV YEAR	INCREASE	
Myers, 1980	sorghum	clay loamy	GEN DEV	INCREASE	
Wang et al., 2005	winter wheat	clay loamy	IRR LEV YEAR	INCREASE	
Feng et al., 2016	maize	loamy clay, clay loam, sandy loam	SOIL YEAR LEV	VARIABLE	VARIABLE
Otto et al., 2014	sugarcane	Typic Kandiudox, Rhodic Eutrudox	SOIL LEV DEV	VARIABLE	
Fang et al., 2022	maize	loamy	LEV YEAR DEV	DECREASE	DECREASE
Louvieaux et al., 2018	oilseed rape		DEV		INCREASE
Nakamura et al., 2002	sorghum		GEN DEV		INCREASE
Comfort et al., 1988	spring wheat	silty loam, clay loam	GEN SITE LEV		INCREASE
Peng et al., 2012	maize	silty loam	DEV LEV YEAR		VARIABLE

DECREASE (in red): diminished R_S, LENG_SHOOT, VARIABLE (in yellow): diverse, inconclusive or no effects on R_S, LENG_SHOOT, and INCREASE (in green): higher R_S, LENG_SHOOT in case of deficient as compared to non-deficient conditions. Factors refer to the variables studied in each manuscript. LEV: several levels of N applied, DEV: several development stages investigated, YEAR: several years investigated, IRR: water treatments applied (such as irrigation and drought), PLAN: several planting methods tested, SOIL: several soil types tested, GEN: diverse genotype tested, SITE: different sites tested, TILL: several tillage practices tested. For more details refer to SI Table A.1.

Table 2.5: Studies that report effects of N deficiency on root diameter (DIA) and specific root length (SRL) at field scale.

Reference	**Crop**	**Soil**	**Factors**	**DIA**	**SRL**
Anderson, 1987	maize	silty loam	DEV YEAR	INCREASE	INCREASE
Sharifi et al., 2005	potato		GEN DEV	VARIABLE	
Eghball and Maranville, 1993	maize	silty clay loam	LEV	DECREASE	
Hadir et al., 2021	sugar beet	silty loam	DEV	DECREASE	
Fang et al., 2022	maize	loamy	LEV YEAR DEV		INCREASE
Nakamura et al., 2002	sorghum		GEN DEV		INCREASE
Anderson, 1988	maize	silty loam	DEV YEAR		VARIABLE
Mehrabi et al., 2021	winter wheat		PLAN IRR LEV		DECREASE

DECREASE (in red): diminished DIA/SRL, VARIABLE (in yellow): diverse, inconclusive or no effects on DIA/SRL, and INCREASE (in green): higher DIA/SRL in case of deficient as compared to non-deficient conditions. Factors refer to the variables studied in each manuscript. LEV: several levels of N applied, DEV: several development stages investigated, YEAR: several years investigated, IRR: water treatments applied (such as irrigation and drought), PLAN: several planting methods tested, SOIL: several soil types tested, GEN: diverse genotype tested, SITE: different sites tested, TILL: several tillage practices tested. For more details refer to SI Table A.1.

Other effects on root morphology

Barber and Mackay (1986) conducted a field experiment with two different maize genotypes in two different soils. The percentage of roots with root hairs was not affected by the amounts of applied N (N0 and N227), but N0 led to a decrease in both root number and root hair length in all maize genotypes.

Schneider et al. (2017) found that maize lines with few-thick nodal roots had smaller total axial root lengths in N0, while lines with many-thin developed a greater total axial root length in N0. The phenotype of fewer, thicker nodal roots was associated with deeper root distribution and resulted in an increased shoot growth under N deficiency.

Maize showed a decrease in the speed of root growth rate (30-49% less) in the topsoil (0-25cm) but an increase (50-60% more) in the subsoil (26-80cm) in treatment N0 compared with N227 at the early growth stage (Barber and Mackay, 1986).

2.4 Phosphorus

A summary of the experimental setup and main effects of P deficiency in root morphology and topology is provided in Table A.2.

Normalized data of root length, root biomass, and root length per shoot biomass differ significantly between P-deficient and non-deficient treatments (Figure 2.3). The differences in root-to-shoot ratio and specific root length were non-significant.

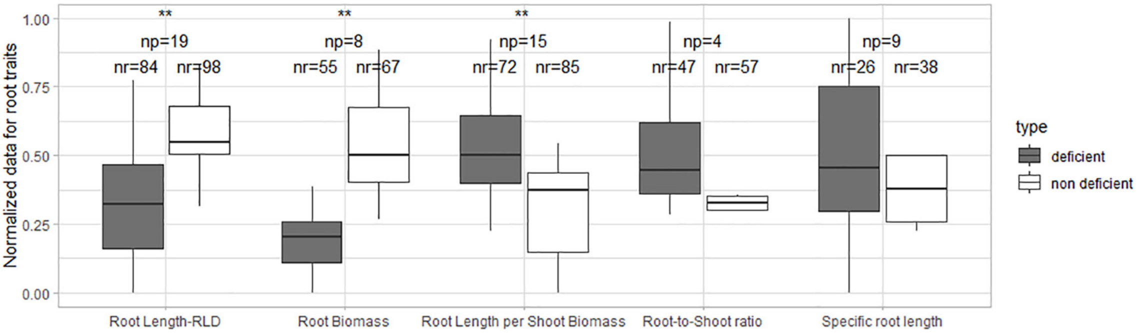


Figure 2.3: Boxplot of the normalized root data under P deficiency and P non-deficiency. A t-test was performed; *s stands for significant differences at a 0.95 confidence level. *np* stands for the number of publications/studies considered in the calculation, and *nr* is the total number of observations within these publications (*np*).

Root length and root length density

Table 2.6 summarizes the studies that report the effects of P deficiency on the total root length or RLD, describing the crop, soil type, factors investigated in each study, and the overall impact. Most studies reported a decrease in root length or root length density under P deficiency (Figure 2.3). This was the case for maize (Sheng et al., 2012; Zhang et al., 2012; Deng et al., 2014), oilseed rape (Duan et al., 2020), sugar beet (Hadir et al., 2021), soybean (Otani and Ae, 1996; Ao et al., 2010), common beans (Ho et al., 2005; Ochoa et al., 2006; Miguel et al., 2015), wheat Teng et al. (2013), as well as for buckwheat, castor, peanut and sorghum (Otani and Ae, 1996). Although all these authors reported a decrease in root length under P deficiency conditions (P0), there are some particularities. For example, in two studies, several (six and eight) P levels were tested. In both cases, root length and/or RLD increased with P-fertilizer rate at first, peaked, and then either declined again in the case of wheat (Teng et al., 2013) or reached a plateau in the case of maize (Deng et al., 2014).

Some studies described that root length was not affected only by P deficiency but also by interactions with other factors. For instance, a genotype effect was found for common beans (Henry et al., 2010b,a; Miguel et al., 2013; Strock et al., 2018) and soybean (Jing et al., 2004). In maize, the level of P deficiency caused diverse effects in RLD (Li et al., 2017). Moreover, the root length of winter barley reacted differently along the development stages at P0 (Steingrobe et al., 2001).

On the contrary, only one study in soybean reported an increase in the root length density in P0, particularly at the topsoil. Nevertheless, no differences were observed in the subsoil (Gutierrez-Boem and Thomas, 1998).

Root biomass

In most studies, deficiency of P supply decreased absolute root biomass (Figure 2.1), as found in maize (Sheng et al., 2012; Zhang et al., 2012; Deng et al., 2014; Li et al., 2017), oilseed rape (Duan et al., 2020), sugar beet (Hadir et al., 2021), wheat (Teng et al., 2013) and common bean (Ochoa et al., 2006). However, a P oversupply could also decrease the root biomass. For instance, in the studies with maize (Deng et al., 2014; Li et al., 2017) and winter wheat (Teng et al., 2013) where several P levels were tested, root dry weight initially increased with increasing soil P supply, reaching its peak and then gradually declined in case of oversupply of P.

Root-to-shoot ratio

Few studies reported the effect of P deficiency on the root-to-shoot ratio (Table 2.7); therefore, it is not possible to conclude about the effect of P deficiency on this trait. An increase in root-to-shoot in P0 compared to high P treatments was found for wheat (Teng et al., 2013) and maize (Deng et al., 2014)). In oilseed rape, the root-to-shoot ratio was higher or smaller depending on the genotype under P stress (Duan et al., 2020). Only one study (in sugar beet) reported a decrease in the root-to-shoot ratio under P deficiency (Hadir et al., 2021).

Root diameter, root diameter distribution, and specific root length

Few studies reported the effect of P deficiency on root diameter distribution (Table 2.7). In maize, a decrease in root diameter was observed in P0 compared to

Table 2.6: Studies that report effects of P deficiency on total root length and/or root length density (TRL-RLD) and root biomass (RBIO) at field scale.

Reference	**Crop**	**Soil**	**Factors**	**TRL-RLD**	**RBIO**
Ho et al., 2005	common beans		GEN IRR	DECREASE	
Miguel et al., 2015	common beans	loamy	GEN	DECREASE	
Ochoa et al., 2006	common beans		GEN	DECREASE	DECREASE
Deng et al., 2014	maize	silty loam	LEV	DECREASE	DECREASE
Sheng et al., 2012	maize	clay loamy	LEV	DECREASE	DECREASE
Zhang et al., 2012	maize	loamy and silt	DEV	DECREASE	DECREASE
Duan et al., 2020	oilseed rape	Alfisol	DEV GEN	DECREASE	DECREASE
Ao et al., 2010	soybean	Acidic red soil	GEN	DECREASE	
Hadir et al., 2021	sugar beet	silty loam	DEV	DECREASE	DECREASE
Teng et al., 2013	wheat	silty	LEV YEAR	DECREASE	DECREASE
Henry et al., 2010b	common beans		GEN IRR	VARIABLE	
Henry et al., 2010a	common beans		GEN	VARIABLE	
Miguel et al., 2013	common beans	loamy	GEN	VARIABLE	
Strock et al., 2018	common beans	silty loam	GEN	VARIABLE	
Li et al., 2017	maize	clay loamy	LEV	VARIABLE	DECREASE
Otani and Ae, 1996	others		CROP	VARIABLE	
Jing et al., 2004	soybean	Acidic red soil	GEN	VARIABLE	
Steingrobe et al., 2001	winter barley	loamy	DEV	VARIABLE	
Gutierrez-Boem and Thomas, 1998	soybean	silty	IRR LEV	INCREASE	

DECREASE (in red): diminished TRL-RLD/RBIO, VARIABLE (in yellow): diverse, inconclusive or no effects on TRL-RLD/RBIO, and INCREASE (in green): higher TRL-RLD/RBIO in case of deficient as compared to non-deficient conditions. Factors refer to the variables studied in each manuscript. LEV: several levels of N applied, DEV: several development stages investigated, YEAR: several years investigated, IRR: water treatments applied (such as irrigation and drought), PLAN: several planting methods tested, SOIL: several soil types tested, GEN: diverse genotype tested, SITE: different sites tested, TILL: several tillage practices tested, CROP: several crops tested. For more details refer to SI Table A.2.

Table 2.7: Studies that report effects of P deficiency on the root-to-shoot ratio (R_S), root length per shoot biomass (LENG_SH), root diameter (DIA), and specific root length (SRL) at field scale.

Reference	**Crop**	**Soil**	**Factors**	**R_S**	**LENG_SH**	**DIA**	**SRL**
Deng et al., 2014	maize	silty loam	LEV	INCREASE	INCREASE		INCREASE
Teng et al., 2013	wheat	silty	LEV YEAR	INCREASE	VARIABLE		
Duan et al., 2020	oilseed rape	Alfisol	DEV GEN	VARIABLE	VARIABLE		INCREASE
Hadir et al., 2021	sugar beet	silty loam	DEV	DECREASI	DECREASE		DECREASE
Zhang et al., 2012	maize	loamy and silt	DEV		INCREASE	DECREAS	VARIABLE
Ho et al., 2005	common beans		GEN IRR		INCREASE		
Miguel et al., 2015	common beans	loamy	GEN		INCREASE		
Henry et al., 2010b	common beans		GEN IRR		INCREASE		
Gutierrez-Boem and Thomas, 1998	soybean	silty	IRR LEV		INCREASE		
Sheng et al., 2012	maize	clay loamy	LEV		VARIABLE	DECREAS	VARIABLE
Henry et al., 2010a	common beans		GEN		VARIABLE		
Jing et al., 2004	soybean	Acidic red soil	GEN		VARIABLE		
Steingrobe et al., 2001	winter barley	loamy	DEV		VARIABLE		
Ao et al., 2010	soybean	Acidic red soil	GEN		DECREASE		VARIABLE
Li et al., 2017	maize	clay loamy	LEV			VARIABLI	VARIABLE
Ochoa et al., 2006	common beans		GEN				INCREASE

DECREASE (in red): diminished effect, VARIABLE (in yellow): diverse, inconclusive or no effects, and INCREASE (in green): higher effect in case of deficient as compared to non-deficient conditions. Factors refer to the variables studied in each manuscript. LEV: several levels of N applied, DEV: several development stages investigated, YEAR: several years investigated, IRR: water treatments applied (such as irrigation and drought), PLAN: several planting methods tested, SOIL: several soil types tested, GEN: diverse genotype tested, SITE: different sites tested, TILL: several tillage practices tested, CROP: several crops tested. For more details refer to SI Table A.2.

the plants that received P fertilizer at the vegetative stage, jointing, and silking (Sheng et al., 2012; Zhang et al., 2012). On the other hand, Li et al. (2017) found no differences in the maize mean root diameter among the tested P treatments.

A P deficiency led to a higher specific root length in oilseed rape (Duan et al., 2020)(Duan et al., 2020), in maize (Deng et al., 2014), and in common bean (Ochoa et al., 2006) (Table 2.7). However, in maize, some specificities were found; for instance, Li et al. (2017) observed a higher SRL in P0 compared with P35 but lower compared with P18. On the contrary, Sheng et al. (2012) reported lower maize SRL in P0 compared with P18 but higher in P35, and Zhang et al. (2012) observed a higher SRL in P0, except before flowering. In soybean, the SRL increased in one genotype under low P and decreased in the other (Ao et al., 2010). Furthermore, in sugar beet, the SRL was smaller in the P0 treatment in a long-term field experiment (Hadir et al., 2021).

Other effects on root morphology

Zhu et al. (2010) found that genotypes with long root hairs under low P availability had significantly higher plant growth, P uptake, specific P absorption rates, and lower metabolic cost-benefit ratios than short-haired genotypes. In this work, root hairs were also longer in the low P treatment.

An increment in relative basal root fraction in common beans at low P was observed by Ho et al. (2005). Steingrobe et al. (2001) grew winter barley in plots that had received 0 and 44 kg P ha-1 over 14 years. The authors observed a faster root production (root dry weight increment per shoot increment) of winter barley in treatments with P0 compared with P44 in all the vegetative stages.

2.5 Potassium

Only six studies that investigated the effect of K deficiency on root growth were identified. A summary of their setup and major findings are described in Supplementary Table A.3.

Normalized data of root length and root length per shoot biomass did not show significant differences in these traits between K-deficient and non-deficient treatments (Figure 2.4). Studies of K deficiency did not provide enough data on root biomass, root-to-shoot ratio, and specific root length to perform statistical analysis. However, some effects are described in the sections below.

Some studies found variable effects on root length and RLD depending on the other studied factors. In barley, Andersen et al. (1992) did not detect significant differences between the medium and high K treatments (K50 and K200) in one year, while in the other year, the root density in the subsoil layers significantly increased by application of high K amounts (K200). In soybean, Fernández et al. (2009) found longer root lengths under low K conditions compared with medium and high K treatments in one of the two years of the experiment, and the root length was smaller in low K treatments in the second year.

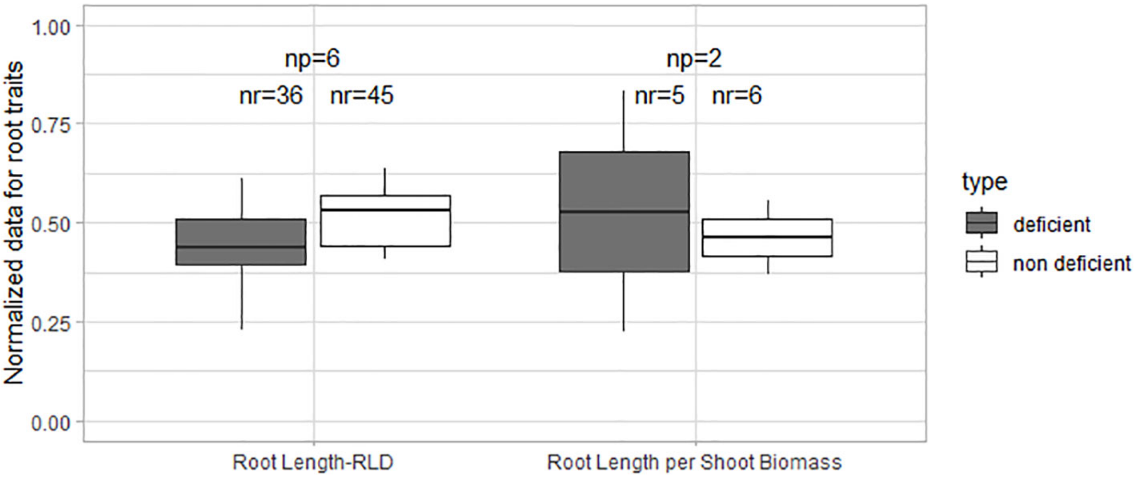


Figure 2.4: Boxplot of the normalized root data under K deficiency and K non-deficiency. A t-test was performed; no significant differences were found. *np* stands for the number of publications/studies considered in the calculation and *nr* the total number of observations within these publications (*np*).

Root biomass, root-to-shoot ratio, and root diameter

K0 led to a decrease in sugar beet root biomass and root-to-shoot ratio in a long-term field experiment (Hadir et al., 2021).

In soybean, a decrease in the average root diameter in low K conditions was observed throughout the growing period (Fernández et al., 2009) and at the seedling and shooting stages (Zhao et al., 2016). The average root diameter was similar in booting and tasseling in the study of Zhao et al. (2016).

Summary of the effects of nutrient deficiencies on root morphological traits

Figure 2.5 summarizes the effects of nutrient deficiencies on five root traits evaluated in this study based on the relative change and normalized values of root traits. Also, the factors that influence contradictory effects in field experiments are listed (Figure 5).

N and P deficiencies in field crop production frequently lead to the reduction of absolute root length, RLD, and absolute root biomass but to an increase of root length per shoot biomass (Figures 1, 5). Moreover, the root-to-shoot ratio increased under low N conditions. Few studies investigated the effects of low P on root-to-shoot, and no statistical differences were found in the normalized data between P deficient and non-deficient treatments. Specific root length was also statistically similar under N and P-deficiency and non-deficiency treatments. The lack of studies on the effects of K deficiency on root morphology limited the assessment of all the traits covered in this review. However, the available data showed that root length and root length per shoot biomass were similar in control and K-sufficient treatments.

Table 2.8: Studies that report effects of K deficiency on total root length and/or root length density (TRL-RLD) at field scale.

Reference	Crop	Soil	Factors	TRL-RLD
Mullins et al., 1994	cotton	sandy loam	YEAR	DECREASE
Zhao et al., 2016	maize	sandy	GEN	DECREASE
Hadir et al., 2021	sugar beet	silty loam	DEV	DECREASE
Andersen et al., 1992	barley	sandy	YEAR DEV	VARIABLE
Valadabadi and Farahani, 2009	maize, sorghum and millet	sandy loam	IRR	VARIABLE
Fernández et al., 2009	soybean	silty loam	YEAR LEV DEV	VARIABLE

DECREASE (in red): diminished TRL-RLD, VARIABLE (in yellow): diverse, inconclusive or no effects on TRL-RLD. Factors refer to the variables studied in each manuscript. LEV: several levels of N applied, DEV: several development stages investigated, YEAR: several years investigated, IRR: water treatments applied (such as irrigation and drought), GEN: diverse genotype tested, SOIL: several soil types tested. For more details refer to SI Table A.3.

2.6 Discussion

The spatial-temporal fluctuations and occurrences of nutrients in the soil are monitored by sensory mechanisms at root tips. This information triggers chemical signals which may shape root growth (Asim et al., 2020). The decrease in root length and root biomass upon N and P deficiency (see also Figures 1-3) seems to be a general property of root morphological plasticity. The low N and P availability negatively affects the above-ground part of the plant, including the leaf area and the photosynthetic capacity per unit of leaf area, consequently leading to a decrease in carbohydrates to be invested in root growth (Postma et al., 2014). Initially, a reduction in photosynthesis might be offset by an increase in the allocation of photosynthates to roots in order to maintain root growth. However, this resource relocation leads to a more pronounced shoot growth reduction, possibly limiting light capture and photosynthesis even more. Eventually, the smaller plants cannot sustain proper root and shoot growth, and absolute root length and biomass decrease.

Noteworthy, the above-mentioned general trend has exceptions. Some studies reported plants with longer roots in low nutrient conditions. In principle, the increase in root length could be a temporary effect in the early development stages (Peng et al., 2012; Xue et al., 2014). On the other hand, it could be that early investment in root growth under low nutrient conditions represents an advantageous strategy to cope with nutrient deprivation, e.g., as a tool to forage into the subsoil (Jia et al., 2022). Several reports indicate that the contribution of subsoil nutrients to overall uptake can be quite variable (Kautz et al., 2013) and also depend on other factors. Those include penetration resistance (Schneider et al., 2017), water distribution in the soil, as well as the availability of other nutrients, e.g., N abundancy when P is

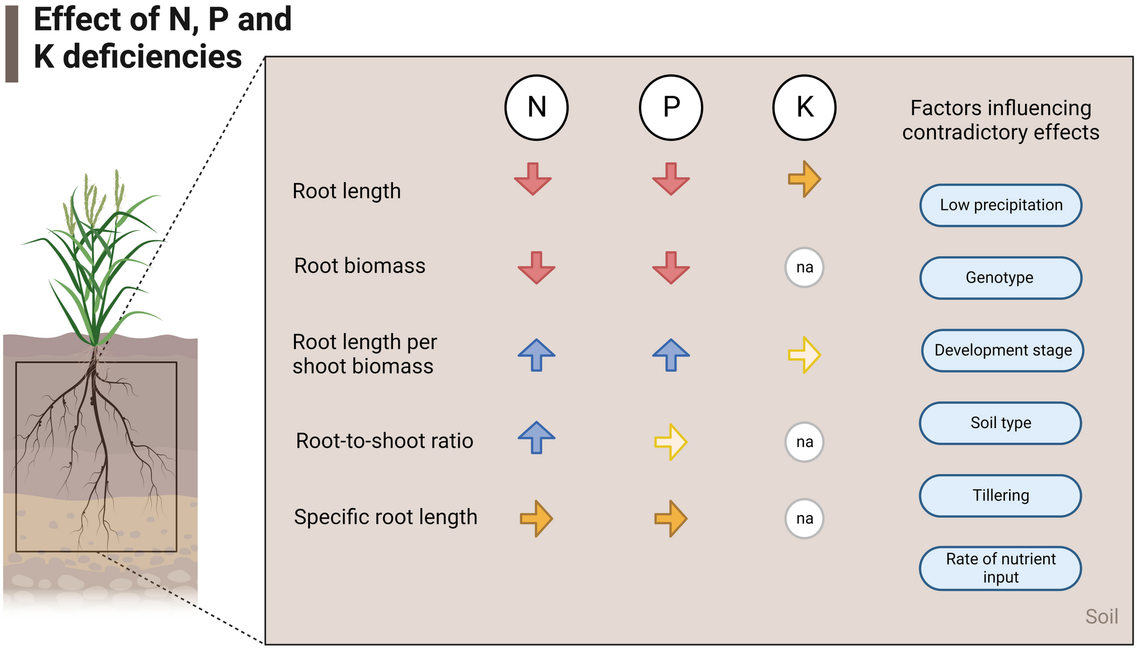


Figure 2.5: Effects of N, P, and K deficiencies at field scale. The red arrows show a decrease, the blue arrows show an increase and the yellow arrows show similarity in that trait in case of deficiency of the respective nutrient. Lighter-colored arrows stand for few studies found investigating that specific parameter (2-4 studies), and na stands for not applicable.

deficient (Bauke et al., 2017).

An apparent effect of N and P deficiencies on root morphology is the higher ratio between root length and shoot biomass. This may be explained by the enormous negative impact of N and P starvation on above-ground biomass, estimated at about 34% of shoot biomass decrease when N or P is deficient. Indeed, the root length also decreases due to the N and P deficiency, but not as much as the shoot biomass. Our review shows a decrease in root length of about 20% for N deficiency and 15% for P deficiency (Figure 1), which is lower than the decrease in above-ground biomass.

Most of the root-to-shoot ratios (Figure 2) increased under N deficiency. It is well known that the root-to-shoot ratio increases under N deficiency due to the concept of functional equilibrium. Competition for carbohydrates and nitrogenous compounds regulates root-to-shoot ratios. For example, when plants are changed from a non-N environment to an N environment with sufficient N supply, the shoot increases its growth in the short term, switching to a lower root-to-shoot ratio and delaying the root growth (Ågren and Ingestad, 1987). On the other hand, when the plant is transferred from a high N level to a zero N level, a non-equilibrium scenario appears; in the beginning, the ratio does not change much as long as free nitrate is available in the tissue, but when the internal nitrate content is depleted, the redistribution of organic-N determines the growth rate (Brouwer, 1983). In that scenario, root growth increases gradually more than shoot growth (Brouwer, 1983). In the end, shoot growth decreases when all the compounds are in N equilibrium. When the plants grow in a prolonged N-deficiency environment, the response to a renewed supply of N decreases (Brouwer, 1983).

Greenhouse (Horst et al., 1996; Shen et al., 2018) and lab studies (Rychter and Randall, 1994; Mollier and Pellerin, 1999; Ciereszko et al., 2011) have shown that the root-to-shoot ratio increases in low P conditions. However, our study could not confirm this finding, possibly due to the sample size (only three studies) which was too small to compare the effect between different conditions.

Specific root length was not affected by N or P deficiency consistently. For example, Ostonen et al. (2007) found a higher SRL in treatments with low nutrient levels. However, this finding was related only to the finest roots, and our review lacks the differentiation of root types. Poorter and Ryser (2015) have analyzed the response of specific leaf area (SLA) to light constraints and the specific root length (SRL) to nutrient availability constraints, as a similar response to constraints above and below ground crop parts, respectively. The changes in SRL were not as significant as SLA changes. However, by separating the root types by function (primary roots from lateral roots), the authors found that low nutrient levels positively affect the SRL of the lateral roots, which are supposedly most active in resource acquisition.

Due to a lack of data, our study can only conclude one consistent result with respect to the effect of K, which is the reduction in root length under K deficiency conditions. This observation can be explained, as in the case of N and P deficiency, with the lower availability of assimilates when K availability is reduced.

Interestingly, the root types monocot and dicot do not only share similar root morphology responses to N and P deficiency but also do so in similar magnitude (see Supplementary Figure S1), despite the differences in their root systems. However, some discrepancies exist in the relative change of root-to-shoot under P deficiency, which was be similar in dicot plants but greater in monocot plants compared with P-added soils. Under K deficiency, the data collected did not support a firm conclusion about the root morphology; however, the decrease in root length differed in magnitude between monocot (approx. 10%) and dicot (approx. 2%). It is similar to the study of Samal et al. (2010), who found a contrast in the magnitude of decrease among some crops tested under K deficiency. Therefore, despite the differences in the root architecture among crops and root types, it is highly likely that the fundamental regulators and sensing mechanisms are similar among monocot and dicot species.

To the best of our knowledge, this study considered all retrievable publications investigating root morphology in common crops at the field scale. Publications involved many soil types, weather conditions, management strategies, and genotypes. Furthermore, we showed findings contradictory to pot experiments and revealed the strengths of field-scale studies. Moreover, due to the meta-analysis of individual observations in each publication, we were able to quantify and statistically support the decrease in root length and biomass and the increase in root length per shoot biomass in low N and P environments. Our study had some limitations, though. None of the studies provided data on all the parameters we investigated. However, some studies had the data needed (such as root biomass, shoot biomass and root length) to calculate root-to-shoot data, root length per shoot biomass, and specific root length. We could calculate these ratios for a better comprehension of the deficiency response.

Nevertheless, the most critical limitation was the incompleteness of information about soil properties and nutrient concentration in the soils and crops in many studies. In this regard, our approach was to classify soil as “deficient” when the nutrient was not applied (0 kg ha-1), which is not necessarily true depending on the soil nutrient content and the needs of a specific crop. Hence, the unfertilized treatment may or may not lead to nutrient deficiency.

Furthermore, our study did not address relevant interactions that may have an impact on the root morphology in the field, for instance, drought, soil temperature, and soil pH. They remain as open questions for further studies. Additionally, studies did not report about root-soil contact and interaction of roots with the rhizosphere microbiome and potential consequences for plant nutrient acquisition (Wendel et al., 2022) which remains a research gap.

2.7 Conclusions

Our study contributes to the knowledge about root adaptation to nutrient-deficient soils. We detected common mechanisms for how root morphology responds to N, P, and K deficiency, even though roots experience multiple interactions simultaneously in the field. Our main findings point out a decrease in root length and biomass but an increase in root length per shoot biomass and root-to-shoot ratio. These findings are particularly interesting for modelling of root growth and agroecosystem, which requires data about the changes in root traits under different nutrient conditions. Future work must now focus on elucidating interactions of nutrient-driven changes in root architectures with other environmental parameters, such as drought, temperature, the soil microbiome, or soil type. Particular focus could be lain on root nutrient plasticity at field scale, since its assessment with high temporal and spatial resolution is nowadays possible with the emerging non-invasive technologies for root phenotyping.

Chapter 3

Winter wheat shoot and root phenotypic plasticity under fertilized and nutrient-deficient field conditions

This chapter has been published as:
Lopez, G., Hadir, S., Mouratidis, S. D., Shuva, M. A., Hüging, H., Bauke, S. L., Gaiser, T., Schaaf, G., & Seidel, S. J. (2025). Winter wheat shoot and root phenotypic plasticity under fertilized and nutrient-deficient field conditions. *European Journal of Agronomy*, 168. `https://doi.org/10.1016/j.eja.2025.127634`

Abstract

While it is widely recognized that nitrogen (N), phosphorus (P), and potassium (K) addition, and liming are crucial for high agricultural yields and soil fertility, field studies examining shoot-root responses to nutrient deficiencies remain limited. Understanding crop adaptation strategies to nutrient-poor soils is crucial for optimizing low-input agriculture. In this study, we investigated the shoot and root responses of winter wheat cultivated in two growing periods (2019/20 and 2020/21) at the long-term fertilizer experiment in Dikopshof, Germany, under no fertilization, or specific omission of N, P, K, and liming with two fully fertilized treatments (NPKCa without and with farmyard manure). We analyzed crop phenology, leaf area index (LAI), plant height, shoot biomass, grain and straw yield, root biomass, root length, root length density (RLD), root-to-shoot ratio (R/ S), specific leaf area (SLA), specific root length (SRL) and root length per shoot biomass. Our results showed that the fully fertilized treatment with manure consistently had the highest values for shoot traits, root length, and root biomass in both growing periods. The unfertilized and N omission treatments led to a decrease in shoot biomass, LAI, plant height, yield, root length, and root biomass while leading to an increase in SRL, R/S, and root length per shoot biomass. The omission of P, K, and liming reduced the straw yield. Our findings highlight the complex interactions between nutrient deficiencies, shoot and root performance, and environmental factors, emphasizing the need for further research on cultivar differences and higher temporal resolution sampling to enhance crop productivity and nutrient management strategies.

3.1 Introduction

The primary function of both above- and belowground structures in plants is to obtain resources for their growth and protection. Although there is general coordination between the allocation and morphology of leaf and root biomass above- and belowground across different species (Enquist and Niklas, 2002), these associations can be significantly altered due to plant phenotypic modifications induced by changing environmental conditions (Freschet et al., 2015; Laughlin et al., 2010). Plants can adapt to their environment by making changes at various levels of integration, such as adjusting the partitioning of biomass among leaves, stems, and roots, modifying the anatomical structures of each organ, and changing the physiological characteristics of the cells that constitute these organs (Freschet et al., 2015; Poorter and Ryser, 2015). Plants likely adjust at all three levels (Poorter and Ryser, 2015). For example, nutrient supply alterations typically result in modifications to functional traits that determine a plant's capacity to obtain resources and overcome the restrictions imposed by the scarce resource (Lynch, 1995).

The aboveground adaptations to nutrient deficiencies in cereals have been widely studied. Studies have reported a decrease in the cereal production of biomass during the growing period and a reduction in yield (and its stability) at harvesting (about 60%) when nitrogen (N) and phosphorus (P) were deficient (Liang et al., 2022; Macholdt et al., 2019). Other studies also reported decreased aboveground biomass for maize (Pandey et al., 2000; Plénet et al., 2000), barley (Hansson et al., 1987), and winter wheat (Wang et al., 2014) when the plants grew in nutrient-poor soils. Specifically, winter wheat yield was affected by about 30% reduction under N deficiency (Zhang et al., 2018), about 55% under P deficiency (Rodríguez et al., 1998), and about 30% under potassium (K) deficiency (Zhang et al., 2020a). In the long-term fertilizer experiment (LTFE), Dikopshof, Seidel et al. (2021) reported a 7% yield loss for winter wheat due to P omission, averaged over the period from 1906 to 2018.

The current knowledge about the effects of nutrient deficiencies on aboveground and, especially, belowground traits, including their ratios, is based mainly on seedling experiments or controlled conditions experiments such as greenhouses or pot experiments (Kravchenko et al., 2017; Rich and Watt, 2013). Due to the nature of sampling in field experiments, these studies are rarely carried out exhaustively. Therefore, there is a knowledge gap in some critical aspects, like the effect of P, K, and lime (Ca) deficiency in plants growing in fields (Lopez et al., 2023). In a recent literature review, Lopez et al. (2023) identified only 50 field-scale studies that explored the effect of nutrient deficiencies on root traits (26 for N, 19 for P, and 5 for K). However, not all of these studies assessed a comprehensive set of root traits; in some cases, only RLD was examined. Among their findings, they showed that N, P, and K deficiency led to a decrease in absolute root length, root length density (RLD), and root biomass in common arable crops. On the other hand, an increase in the root-to-shoot ratio (R/S) and root length per shoot biomass ratio under N and P deficiency was reported (Lopez et al., 2023). Specifically, roots of winter wheat showed a decrease in root length and root biomass under N and P deficiency. Deficiency of N resulted in a reduction of root length by approximately 10% and root biomass by about 3% (Barraclough et al., 1989; Comfort et al., 1988; Mehrabi et al., 2021; Wang et al., 2014; Xue et al., 2014), while P deficiency led to a decrease of about 20% in root length and 10% in root biomass (Teng et al., 2013). Wheat R/S and root length per shoot biomass were higher in nutrient-deficient soils (Lopez et al., 2023).

Field-scale studies, particularly those conducted over multiple years, often encounter variability in their results. This variability can arise from various factors, such as weather conditions, soil characteristics, and management practices, which can fluctuate yearly (Kravchenko et al., 2017). While these factors also vary across years in long-term field experiments (LTFEs), the major advantage of LTFEs lies in their ability to provide long time series of data. These data are crucial for interpreting the results of short-term studies, understanding trends, and assessing the long-term build-up of treatment or management effects (Johnston and Poulton, 2018). Furthermore, the treatments used in LTFEs allow for the detailed study of specific management practices and their interactions, making them useful for understanding crop responses and refining agricultural practices over time.

To the best of our knowledge, only six studies have investigated root adaptations to nutrient deficiency in long-term field experiments (Hadir et al., 2020; Pellerin et al., 2000; Sheng et al., 2012; Steingrobe et al., 2001; Zhang et al., 2012; Zhao et al., 2016). Among their findings, Pellerin et al. (2000) found that P-deficient maize plants exhibited a lower and delayed emergence of adventitious roots. Sheng et al. (2012) found that P fertilization reduced arbuscular mycorrhizal fungal colonization while increasing RLD and the percentage of fine roots in maize. Zhang et al. (2012) observed that P-deficient maize exhibited reduced growth rate, increased P use efficiency, and developed more thin roots with a diameter less than 0.6 mm compared to maize treated with sufficient P. Regarding K deficiency, Zhao et al. (2016) discovered that the K-tolerant maize line had significantly higher root length, volume, and surface area compared to the K-sensitive line under K-treatment. Steingrobe et al. (2001) found that winter barley shoot development and grain yield were reduced under P deficiency, but the standing root system size remained similar to the P-fertilized treatment (although total root production was higher in the P-deficient treatment, root mortality was also higher). In sugar beet, a decrease of RLD was found under N, P and K deficiency (Hadir et al., 2020).

We aim to answer how the above- and belowground traits of winter wheat react to the lack of nutrients. Specifically, we are interested in the aboveground traits such as: shoot biomass, leaf area index (LAI), plant height and grain and straw yield. And belowground traits such as: root biomass, total root length, RLD, root mass density (RMD), average root diameter, root length distribution, and link connectivity. Also, we are interested in the main ratios to evaluate the performance of the crop under nutrient-poor conditions, such as specific leaf area (SLA), specific root length (SRL), R/S, and root length per shoot biomass. Beyond examining individual traits, we aim to assess the strength and nature of correlations between shoot and root traits. We also aim to assess the correlations between shoot traits, root traits, and soil nutrient content through Pearson correlation analysis, as well as to evaluate multivariate patterns among traits using PCA to identify how nutrient treatments shape trait interactions.

In line with existing literature, we hypothesize that nutrient deficiencies will lead to reductions in shoot biomass, LAI, root biomass, and root length while increasing the ratios (SLA, SRL, R/S, and root length per shoot biomass) as adaptive responses to nutrient stress.

For this purpose, we have conducted a two-year field campaign in the LTFE Dikopshof, established in 1904, which includes plots maintained under different fertilization treatments: complete fertilizer application (NPKCa), the complete fertilizer treatment plus manure, N fertilizer omission, P fertilizer omission, K fertilizer omission, Ca omission, as well as unfertilized plots, creating soil conditions with varying nutrient deficiencies.

3.2 Materials and Methods

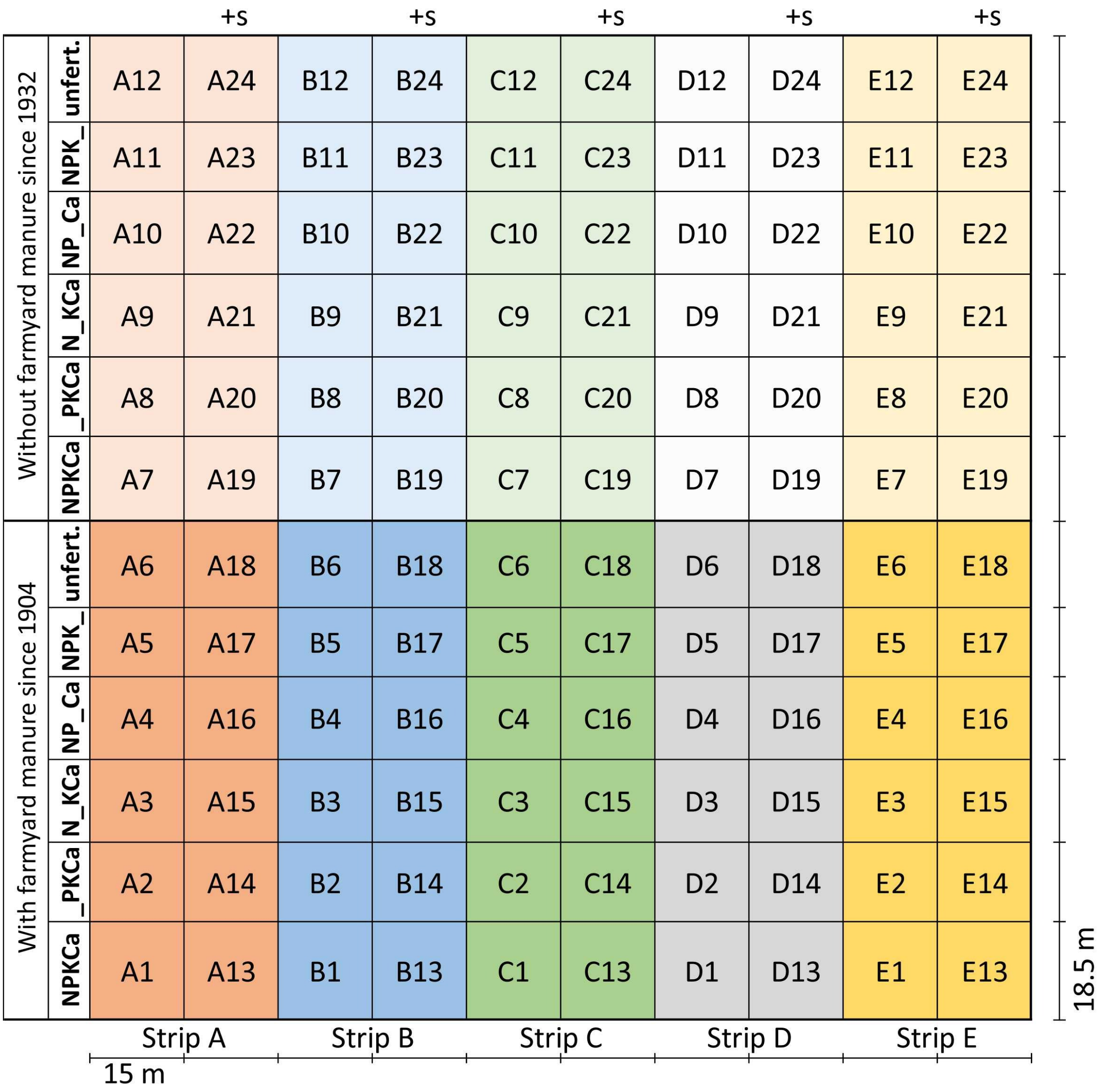
3.2.1 Site description

The field study was carried out in the LTFE Dikopshof during the growing period of winter wheat 2019/20 (growing period 1) and 2020/21 (growing period 2). The LTFE Dikopshof was established in 1904 near Cologne, Germany (50°48′21″ N, 6°59′9″ E; altitude: 61 m), located at the intermediate terrace of the Rhine river. This LTFE is the tenth oldest in the world (Körschens, 2021). The groundwater table is about 20 m below the surface. The Atlantic climate with mild winters and summers results in a mean annual temperature of 10.1 °C and a mean annual precipitation of 630 mm. The general soil type is classified as a Haplic Luvisol derived from loess above sand (Holthusen et al., 2012). The depth of the loess layer in the experimental field varies from 1.1 m to 1.3 m and is followed by gravel layers. The soil texture can be described as silty loam (topsoil) and (silty) clay loam (below 30 cm soil depth). Soil bulk density ranged from about 1.4 g cm^{-3} in the topsoil to about 1.5–1.6 g cm^{-3} below 30 cm soil depth.

3.2.2 Experimental design and management

The five-year crop rotation at the LTFE Dikopshof comprises *Beta vulgaris*, *Triticum aestivum* L., *Secale cereale* L., a fodder legume, and *Avena sativa* L./*Solanum tuberosum* L. (potato replaced oat in 1953). The fodder crop initially used was *Trifolium pratense*, then *Medicago sativa*, and, after 1967, mainly *Trifolium resupinatum* L. In each of the five strips (A to E), one of the five crops of the rotation is grown (Fig. 3.1).

The experiment is a non-randomized block design without replicates (see experimental design in Fig. 3.1) and comprises six core treatments: NPKCa, _PKCa, N_KCa, NP_Ca, NPK_, and unfertilized (_ stands for the omission of the corresponding nutrient). In addition to these core treatments, three additional variants exist for each: (1) with farmyard manure (FMY) application (+m), (2) with supplemental synthetic fertilizer application introduced since 1953 (+s), and (3) with both FMY and supplemental synthetic fertilizer application (+m+s). The nutrient amounts applied in the +m and +s variants are equivalent, with the +s treatment designed



			+s		+s		+s		+s		+s
Without farmyard manure since 1932	**unfert.**	A12	A24	B12	B24	C12	C24	D12	D24	E12	E24
	NPK_	A11	A23	B11	B23	C11	C23	D11	D23	E11	E23
	NP_Ca	A10	A22	B10	B22	C10	C22	D10	D22	E10	E22
	N_KCa	A9	A21	B9	B21	C9	C21	D9	D21	E9	E21
	_PKCa	A8	A20	B8	B20	C8	C20	D8	D20	E8	E20
	NPKCa	A7	A19	B7	B19	C7	C19	D7	D19	E7	E19
With farmyard manure since 1904	**unfert.**	A6	A18	B6	B18	C6	C18	D6	D18	E6	E18
	NPK_	A5	A17	B5	B17	C5	C17	D5	D17	E5	E17
	NP_Ca	A4	A16	B4	B16	C4	C16	D4	D16	E4	E16
	N_KCa	A3	A15	B3	B15	C3	C15	D3	D15	E3	E15
	_PKCa	A2	A14	B2	B14	C2	C14	D2	D14	E2	E14
	NPKCa	A1	A13	B1	B13	C1	C13	D1	D13	E1	E13
		Strip A		Strip B		Strip C		Strip D		Strip E	

Figure 3.1: Experimental setup of the long-term fertilizer experiment at LTFE Dikopshof after 1953 (strips A to E). The arabic numbers stand for the treatments. Since 1932, no replicates are available. The experiment is not randomized. Treatment ID 7: NPKCa, 8: _PKCa, 9: N_KCa, 10: NP_Ca, 11: NPK_, 12: unfertilized and 13: NPKCa+m+s. Each color represents a strip. Darker colors represent the plots where farmyard manure is applied, and lighter colors represent the plots without farmyard manure application.

to compensate for the nutrients supplied by FMY in the +m treatment. The inclusion of the NPKCa+m+s treatment represents the highest nutrient input, reflecting fertilization practices comparable to those currently used in surrounding farms. The fertilizer inputs of the other treatments are lower (and below common amounts applied in conventional farming) as they were fixed in 1906 (partly adapted in 1953) and kept static since then. A total of 60 t ha^{-1} of fresh cattle manure is applied per rotation (20 t ha^{-1} before sugar beet, winter rye, and potato), distributed after harvesting the preceding crop (five-year rotation mean since 1953, treatments "+m"). In total, the experiment consists of five strips with 24 treatments per strip (120 plots). The fertilization management has not changed since 1953, except for a slight increase of the N fertilizer application (+30 kg N ha^{-1}) on winter wheat in some treatments, which occurred in the 1980s. The fertilizer amounts applied in winter wheat and in the whole rotation can be seen in Table 3.1. Crop residues and stubble are removed during the entire period, except for roots and senesced potato leaves. Since 1909, the regular depth of plowing has been 30 cm. The plot size is 18.5 × 15 m with a core plot of 10 × 9 m. For more specifics and a detailed list of all crops per strip and year until 2018, please refer to the supplementary information of the study conducted by Seidel et al. (2021). The considered plots cultivated with winter wheat are plots B7 to B13 in strip B (2019/20) and A7 to A13 in strip A (2020/21) shown in Fig. 3.1.

Table 3.1: Considered fertilization treatments and fertilizer application rates (N, P, K, and Ca) in winter wheat and in the whole crop rotation (rotation sum) in the LTFE Dikopshof. Base and supplemental fertilizers are mineral fertilizers. +m stands for manure (nutrients applied via cattle farmyard manure).

		Application rate per element							
		Winter Wheat (kg ha^{-1} yr^{-1})				Rotation Sum (kg ha^{-1})			
Treatment	**Type of fertilizer**	**N**	**P**	**K**	**Ca**	**N**	**P**	**K**	**Ca**
NPKCa+m+s	Base	120	31	116	0	290	155	580	1143
	+m					120*	66	249	150
	+s					120	66	249	0
NPKCa	Base	60	31	116	0	230	155	580	1143
PKCa	Base	0	31	116	0	0	155	580	1143
N_KCa	Base	60	0	116	0	230	0	580	1143
NP_Ca	Base	60	31	0	0	230	155	0	1143
NPK_	Base	60	31	116	0	230	155	580	0
unfertilized	Base	0	0	0	0	0	0	0	0

*N in manure refers to total N.

3.2.3 Crop management and sampling

In this study, winter wheat was grown under various treatments: NPKCa+m+s, NPKCa, _PKCa, N_KCa, NP_Ca, NPK_, and an unfertilized treatment. Winter wheat (variety Boss) was sown on 25th November 2019 and harvested on 4th August 2020 in the growing period 1 (2019/20) and sown on 6th November 2020 and harvested on 13th August 2021 in the growing period 2 (2020/21). The dates of the field campaigns (growing periods 1 and 2), along with the sampled crop traits and the soil characteristics measured during each campaign, are presented in Table 3.2. Each sampling within each plot was measured four times due to the non-randomized block design of the experiment.

Table 3.2: Dates of field campaigns and phenological traits measured during the winter wheat growing period 1 (2019/20) and 2 (2020/21)*

	Date	BBCH	Phenology	Height (cm)	S_Biomass (t ha^{-1})	LAI (m^{2} m^{-2})	N_Till_Ears	Yield (t ha^{-1})	Soil_Moist (%)	Soil	Roots
Growing period 1 (2019/20)	17/03/20	23	tillering	x	x	x				x	x
	30/03/20	23–24	tillering	x							
	07/04/20	24–25	tillering		x	x					
	22/04/20	31	stem elongation	x	x	x					
	07/05/20	32–37	stem elongation	x	x	x					
	19/05/20	39–45	booting	x	x	x			x	x	x
	26/05/20								x		
	02/06/20	65–69	flowering	x					x		
	09/06/20								x		
	17/06/20	83–84	ripening	x			x		x		
	23/06/20								x		
	04/08/20	89	ripening					x			
Growing period 2 (2020/21)	05/05/21	24–28	tillering	x	x	x			x		
	19/05/21								x		
	02/06/21								x		
	08/06/21	57–59	heading	x	x	x					
	16/06/21								x		
	28/06/21	69	flowering	x	x	x	x			x	x
	13/08/21	89						x			

*BBCH = phenological stage, Height = plant height, S_Biomass = shoot biomass, LAI = leaf area index, N_Till_Ears = number of tillers or ears, Yield = grain and straw yield, Soil = soil nutrient content (C, N, Nmin, Pcal, Kcal, pH), Soil_Moist = soil moisture, Roots = roots traits that comprise RLD, RMD, R/S, SRL, root diameter classes, and root link analysis.

The presented crop, soil and root data comprise:

- Soil total C (%), total N (N_t) (%), soil mineral N (N_{min}) (kg ha^{-1}), plant available P (P_{cal}) (mg kg^{-1}) and K (K_{cal}) (mg kg^{-1}), and pH values
- Volumetric soil water content (%)
- Phenological development stages (BBCH stage)
- Plant height (cm)
- Leaf area index (LAI) (m^2 m^{-2})
- Dry matter shoot biomass (t ha^{-1})
- Number of tillers and ears per m^2
- Grain and straw yield (t ha^{-1})
- Total root length (cm)
- Average root diameter (mm)
- Root length density by soil layer (RLD) (cm cm^{-3})
- Total root biomass (t ha^{-1})
- Root mass density by soil layer (RMD) (mg cm^{-3})
- Distribution of root length by diameter classes (%)
- Link connectivity (cm cm^{-1})
- Root-to-shoot ratio (R/S)
- Specific leaf area (SLA) (m^2 kg^{-1})
- Specific root length (SRL) (m g^{-1})
- Root length per shoot biomass (km kg^{-1})

The growing period 1 (2019/20) was drier and warmer compared with the growing period 2 (2020/21) (Fig. B.1 in supplementary information (SI)). The rainfall during growing period 1 (2019/20) was scarce even in the months where it is usually more abundant (July), otherwise the growing period 2 (2020/21) had greater amounts of rainfall and lower mean temperatures. On 14th July 2021, a heavy rainfall event occurred with 120 mm of precipitation.

3.2.4 Soil sampling and analysis

Soil samples were collected using a Pürckhauer auger, with four replicates per treatment, and divided by layer (0–30 cm, 30–50 cm, and 50–100 cm). The samples were then pooled per treatment and frozen. After thawing, the soil was analyzed for N_{min} by extraction with potassium sulfate solution. N_{min} concentrations in the extracts were measured by a Skalar Continuous Flow Analyser (Skalar Analytical B.V., Breda, Netherlands). Moreover, the soil samples were prepared by drying and sieving, and the contents of C_{org}[1] and N_t were determined using elemental analysis (Euro-EA elemental analyzer from HEKAtech GmbH). P_{cal} and K_{cal} were determined using a calcium acetate–lactate extract as described in Schüller (1969). P concentration in the extracts was determined colorimetrically following molybdenum blue reaction (Murphy and Riley, 1962) on a spectrophotometer (Specord 205, Analytik Jena, Germany). K concentration in the extracts was determined by atomic absorption spectroscopy (novAA 400 P, Analytik Jena, Germany). In addition, the pH of the soil samples was determined using a $CaCl_2$ solution and a pH Meter Multi 3630 IDS from WTW and Sentix 940 P electrode.

Soil moisture content was determined using the FDR moisture sensor HH2 within ML3 Theta Probe (ecoTech Umwelt-Meßsysteme GmbH, Bonn, Germany). Measurements were taken at various soil depths up to 90 cm soil depth. The measurements were conducted directly on the rows after the biomass sampling. See Table 3.2 for the days of sampling.

3.2.5 Shoot observations

BBCH

The BBCH-scale (Biologische Bundesanstalt, Bundessortenamt und CHemische Industrie) was used to visually identify the phenological development stages of winter wheat per treatment.

Plant height in cm

Plant height was measured in the field using a ruler, with measurements taken from the soil surface to the top of the plant without applying any force to stretch the leaves upwards. For each treatment, plant height was measured on 10 plants, and the mean value was calculated.

Leaf area index in m^2 m^{-2} and shoot biomass in t ha^{-1}

The LAI was determined destructively. For that, the plants (entire shoot) of an area of 1 m^2 (four replicates per treatment) were cut and separated into specific organs, including leaves, stems, and ears. The separated parts were then brought to the

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[1] Total carbon was analyzed, and since the soil contains no carbonates, the total C measurement corresponds entirely to organic carbon (C_{org}).

laboratory and scanned using the LI-3100C Area Meter (Li-Cor). The shoot LAI was calculated for each 1 m^2. The shoot dry matter was determined by oven-drying (at 105 °C) the samples used to estimate the LAI. The dry biomass was then scaled up to tons per hectare.

Grain and straw yield in t ha^{-1}

Yield was determined by harvesting three 15 m^2 areas using a machine that threshed the wheat and separated the straw from the grains. The straw and grains were weighed, and a subsample was taken to the laboratory to estimate moisture content and adjust the yield weight. Both the straw and grain yields were then converted to tons per hectare.

Number of tillers and ears

Plants, tillers, and ears per plant were enumerated manually in four separate locations within each treatment, each conducted in a 1 m^2 area.

Specific leaf area in m^2 g^{-1}

SLA was calculated based on Eq. 3.1. For this calculation, only the leaf area and biomass of the leaves were considered due to the previous separation of the organs while processing.

$$\text{SLA} = \frac{\text{Leaf surface area (m}^2\text{)}}{\text{Dry leaf biomass (g)}} \tag{3.1}$$

3.2.6 Root sampling, preparation and scanning

Roots of winter wheat plants were extracted twice during growing period 1 (on March 17 and May 19, 2020) and once during growing period 2 (on June 28, 2021) using a root auger with an inner diameter of 9 cm and a length of 1 m. Soil cores were divided into 10 cm segments (0–10 cm, 10–20 cm, . . . , 90–100 cm) and placed in plastic bags. Four measurements were collected from each plot, consisting of two samples (measurements 1 and 2) taken within the row (in-row) and two samples (measurements 3 and 4) taken between adjacent rows (between-row). Before sampling, the surrounding area of each sampling point was visually inspected to ensure the absence of any weeds.

The soil samples containing winter wheat roots (280 samples per date) were refrigerated and processed sequentially. To separate the roots from the soil, the samples were soaked in tap water and hand-washed using sieves with mesh sizes of 1 mm, 0.83 mm, and 0.5 mm to remove the coarsest soil and debris. The use of multiple sieve sizes ensured that fine roots were included while allowing the larger sieves to retain most of the roots, making the cleaning process more efficient. Subsequently, the roots were sorted with tweezers, to remove the smallest particles and dead roots.

After cleaning, all roots from the different sieves were combined and stored in tap water at 3 °C until scanning.

Roots were scanned using an EPSON scanner (HP Expression 1100XL). Each sample's roots were arranged in an acrylic glass platter filled with tap water, scanned, and analyzed using WinRHIZO (see scanning settings in Fig. B.2 in SI) software (version Pro 2020a, Regent Instruments, Quebec, Canada). The total root length and average root diameter per sample were directly estimated using WinRHIZO software.

Total root length (cm) and average root diameter (mm)

The total root length and average root diameter per sample were directly estimated using WinRHIZO software.

Root length density by soil layer (cm cm^{-3})

To calculate RLD, the total root length (in cm) was divided by the volume of the core sample, which is 636.17 cm^3 (calculated based on a radius of 4.5 cm and height of 10 cm):

$$\mathrm{RLD} = \frac{\text{Root length in the soil sample (cm)}}{\text{Volume of the soil sample (cm}^3\text{)}} \tag{3.2}$$

Root biomass (t ha^{-1})

After analysis, the root weight per soil layer and replicate was determined by drying the roots at 60 °C and weighing the dried roots. Then, the root biomasses per layer were added to calculate the total root biomass for the core profile (1 m depth). The total root biomass was divided by the area of the core (63.52 cm^2) converted to tons per hectare, and then averaged across the four sampling points within each treatment:

$$\mathit{Root\ biomass} = \frac{\text{Dry root biomass of the entire soil core (t)}}{\text{Area of the soil core (ha)}} \tag{3.3}$$

Root mass density by soil layer (mg cm^{-3})

To calculate RMD, the root biomass per layer was divided by the volume of the core sample (636.17 cm^3) and converted to mg per cm^3:

$$\mathrm{RMD} = \frac{\text{Dry root biomass in the soil sample (mg)}}{\text{Volume of the soil sample (cm}^3\text{)}} \tag{3.4}$$

Root-to-shoot ratio

The R/S was calculated by dividing the total root biomass (t ha^{-1}) by the shoot biomass (t ha^{-1}):

$$R/S = \frac{\text{Dry root biomass (t ha}^{-1}\text{)}}{\text{Dry shoot biomass (t ha}^{-1}\text{)}} \tag{3.5}$$

Specific root length (m g^{-1})

SRL was calculated by dividing the total root length (m) by the total dry root biomass (g):

$$\text{SRL} = \frac{\text{Total root length (m)}}{\text{Total dry root biomass (g)}} \tag{3.6}$$

Root length per shoot biomass (km^2 kg^{-1})

It was calculated by dividing the total root length (km) by the shoot biomass (kg):

$$Root\ length\ per\ shoot\ biomass = \frac{\text{Total root length (km)}}{\text{Dry shoot biomass (kg)}} \tag{3.7}$$

Distribution of Root Length by Diameter Classes

WinRHIZO software was used to estimate the sample's root length per diameter class. Based on these results, the root length (per sample) was calculated for three classes: very fine (diameter < 0.15 mm), fine (diameter between 0.15 and 0.6 mm), and medium (diameter > 0.6 mm). The length per diameter class was calculated and plotted as the length of a diameter class per total length in the sample.

Link connectivity

Five root systems within a top- and subsoil layer were selected and processed with WinRHIZO for link analysis. Link analysis categorizes root segments (links) into three different groups: exterior-exterior (EE), exterior-interior (EI), and interior-interior (II) (see a sketch of the link types in Fig. B.3). The length per link type divided by the total length (in the five root systems) was calculated and plotted. More details on the method can be found in Fitter and Stickland (1991).

3.2.7 Statistical data analyses

The data obtained from the experiment were analyzed using R software (version 4.0.2). Due to the lack of true replication in the experimental setup, we present the data as descriptive statistics, reporting only the mean and standard deviation to show the variability within each treatment. Our analysis focuses on comparing each nutrient-deficient treatment with the fully fertilized treatment (NPKCa) to evaluate the effects of nutrient deficiencies.

Also, for the days when shoot and root were sampled, Pearson's correlation coefficient was calculated to find the linear association between the soil parameters (pH, C_{org}, N_t, N_{min}, P_{cal}, and K_{cal}), above- and belowground (only total root length, root biomass, and average root diameter) variables. Pearson analysis was conducted for the entire soil profile (average), topsoil (0–30 cm depth), and subsoil (below 30 cm depth). A detailed description of this statistical analysis can be found in Kirch (2008). For the entire soil profile approach, the average of the soil values were used, except for the first sampling date in 2020 (March 17th, 2020), where only data from the 0–30 cm depth range were available.

In order to compare the differences between treatments, we calculated the relative changes in shoot and root traits using the mean values of the sampling points within each treatment, with the NPKCa treatment as the baseline. The included traits were: grain yield, straw yield, shoot biomass, total root biomass, total root length, SLA, SRL, R/S, and root length per shoot biomass. We compared the treatments within the same growing period and BBCH stage. In summary, we used graphical indicators: green arrows indicating higher values compared to the baseline, yellow arrows representing similar values (ranging from -5 to 5 %),2 and red arrows denoting lower values compared to the baseline.

For the days when shoot and root samples were taken (two in growing period 1 and one in growing period 2), we included a Principal Component Analysis (PCA) to evaluate the relationships and variability among traits measured. PCA reduces the dataset's dimensionality while preserving its variability, enabling the identification of patterns, correlations, and treatment clustering. The analysis incorporated key variables: pH, C_{org}, N_t, N_{min}, P_{cal}, K_{cal}, plant height, LAI, shoot biomass, root biomass, total root length, RLD, RMD, average root diameter, R/S, root length per shoot biomass, SRL, and SLA. PCA was conducted using the `FactoMineR` package in R. Visualization of the PCA results was performed with the `factoextra` package.

3.3 Results

3.3.1 Belowground parameters and their response to soil nutrients

Soil water content

Throughout both growing periods, the NPKCa treatment exhibited moderate soil water content, with lower values in 2019/20 (11.8 % for topsoil and 16.2 % for subsoil) than in 2020/21 (18 % for topsoil and 18.2 % for subsoil). In both years, the unfertilized and _PKCa treatments consistently showed higher soil water content across the soil profile compared to NPKCa. In contrast, the NPKCa+m+s treatment exhibited lower soil water content levels. The N_KCa, NP_Ca, and NPK_ treatments displayed fluctuating soil water content, with variations between increases and decreases relative to NPKCa depending on the measurement date and soil depth (Tables B.1 and B.2).

Soil nutrient content

Across all soil layers and sampling dates, the NPKCa+m+s treatment consistently showed the highest nutrient levels (N_{min}, K_{cal}, and P_{cal}). In contrast, the unfertilized treatment displayed the lowest nutrient content and pH levels. Specific deficiencies were observed in particular treatments: N_KCa often had the lowest P_{cal} levels, NP_Ca frequently had the lowest K_{cal} levels (Tables B.3, B.4 and B.5).

Total root length and root length density

Throughout all growing periods and BBCH stages, the total root length of the _PKCa and unfertilized treatments was consistently lower than that of the NPKCa treatment. Additionally, the NPKCa+m+s and NPK_ treatments showed similar or even greater total root lengths compared to the NPKCa treatment (see Fig. 3.2 and for detailed information, refer to Table B.6, B.7, and B.8). The differences are also illustrated in Fig. 3.3, which displays the distribution of RLD throughout the entire soil profile.

At tillering in growing period 1 (2019/20 – BBCH 23), the RLD of the NPKCa treatment was 0.98 cm cm^{-3} in the topsoil and 0.07 cm cm^{-3} in the subsoil. Only the NPK_ treatment exhibited a greater RLD, showing a 12 % increase in both the top and subsoil compared to NPKCa. Most of the other treatments, including NPKCa+m+s, _PKCa, N_KCa, NP_Ca, and the unfertilized treatments, displayed lower RLD values, varying from 6 % to 78 % in both topsoil and subsoil.

At booting of growing period 1 (2019/20 – BBCH 43), the root length density (RLD) for the NPKCa treatment was 2.29 cm cm^{-3} in the topsoil and 1.30 cm cm^{-3} in the subsoil. At flowering of growing period 2 (2020/21 – BBCH 69), these values were 2.12 cm cm^{-3} in the topsoil and 0.58 cm cm^{-3} in the subsoil. Treatments such as NPKCa+m+s, N_KCa, NP_Ca, and NPK_ exhibited higher total root lengths and RLDs than NPKCa in both soil layers. Increases ranged from 1 % to 62 % at booting and from 37 % to 106 % at flowering in the topsoil. In the subsoil, the increases were between 5 % and 27 % at booting and between 82 % and 209 % at flowering. In contrast, the unfertilized and _PKCa treatments showed lower RLDs compared to NPKCa, with reductions of 20–30 % in the topsoil and 25–47 % in the subsoil across both growth stages.

Root biomass and root mass density

Throughout all growing periods and BBCH stages, the _PKCa and unfertilized treatments consistently showed lower total root biomass compared to the NPKCa treatment. In contrast, the NPKCa+m+s treatment exhibited greater root biomass values relative to NPKCa. The N_KCa, NP_Ca, and NPK_ treatments displayed

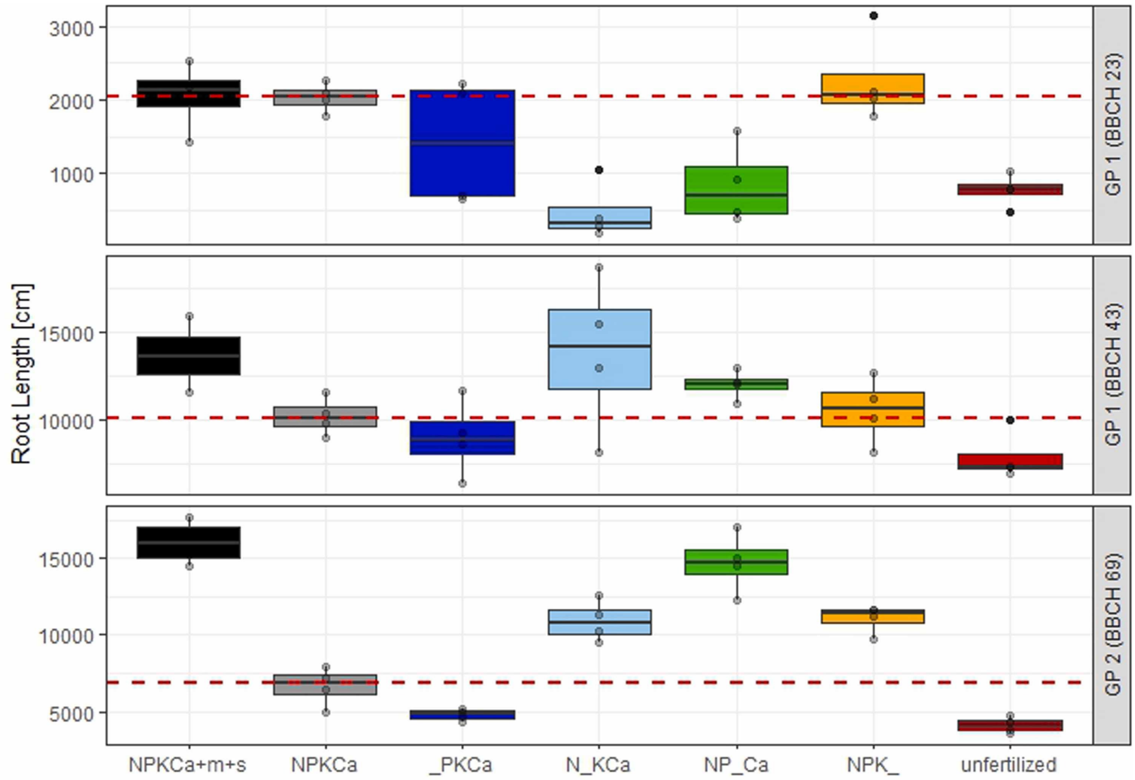

Figure 3.2: Total root length (cm) across different treatments during GP1: growing period 1 (2019/20 - BBCH 23), growing period 1 (2019/20 - BBCH 43) and GP2: growing period 2 (2020/21 - BBCH 69). The red dashed line represents the median root length of the NPKCa treatment as a baseline for comparison. Boxplots indicate the variability and median root length within each treatment.

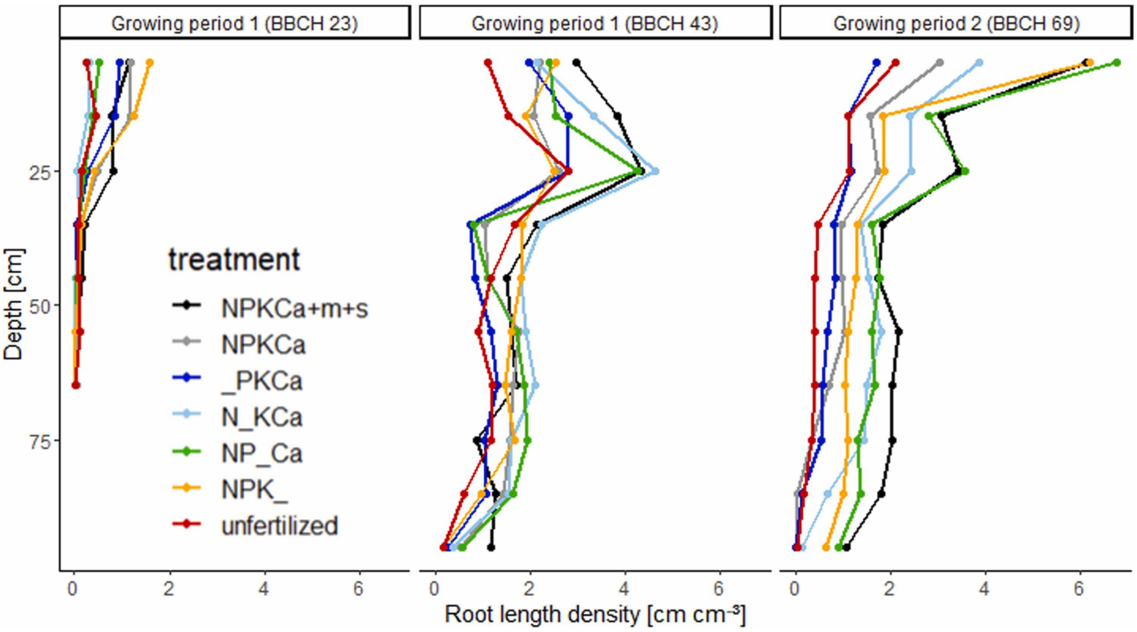

Figure 3.3: Observed mean (n=4) root length density (cm cm^{-3}) in seven treatments of the LTFE Dikopshof, Germany, for growing period 1 (2019/20 - BBCH 23), growing period 1 (2019/20 - BBCH 43) and, growing period 2 (2020/21 - BBCH 69). Standard deviation within each treatment is shown in SI in Table B.6, B.7, and B.8.

variable results (see Fig. 3.4 for reference and detailed information in Tables B.6, B.7, and B.8). The differences are also illustrated in Fig. 3.5, which displays the distribution of RMD throughout the entire soil profile. Additionally, a figure showing both above- and belowground biomass is presented in Fig. S4 of the SI.

When examining the different soil profiles (Fig. 3.5), at tillering in growth period 1 (2019/20 – BBCH 23), at booting in growth period 1 (2019/20 – BBCH 43), and at flowering in growth period 2 (2020/21 – BBCH 69), the RMD of NPKCa+m+s was greater (by between 2 % and 44 %) than the RMD of NPKCa in the topsoil. The treatments with _PKCa and the unfertilized areas exhibited lower RMD in both the topsoil and subsoil across all growth periods. Additionally, N_KCa, NP_Ca, and NPK_ treatments showed higher RMD at booting (only topsoil) and at flowering (only subsoil).

Root length distribution based on average root diameter

During growing period 1 (2019/20 - BBCH 23), treatments N_KCa and unfertilized showed that more than 50% of the total root length consisted of very fine roots (diameter less than 0.15 mm). The remaining treatments had approximately 30–40% of very fine roots. For growing period 1 (2019/20 - BBCH 43) and growing period 2 (2020/21 - BBCH 69), the root length distribution was similar across all treatments, with around 50% of very fine roots in growing period 1 (2019/20 - BBCH 43) and around 20% in growing period 2 (2020/21 - BBCH 69) (see Fig. B.5 in the supplementary material for details).

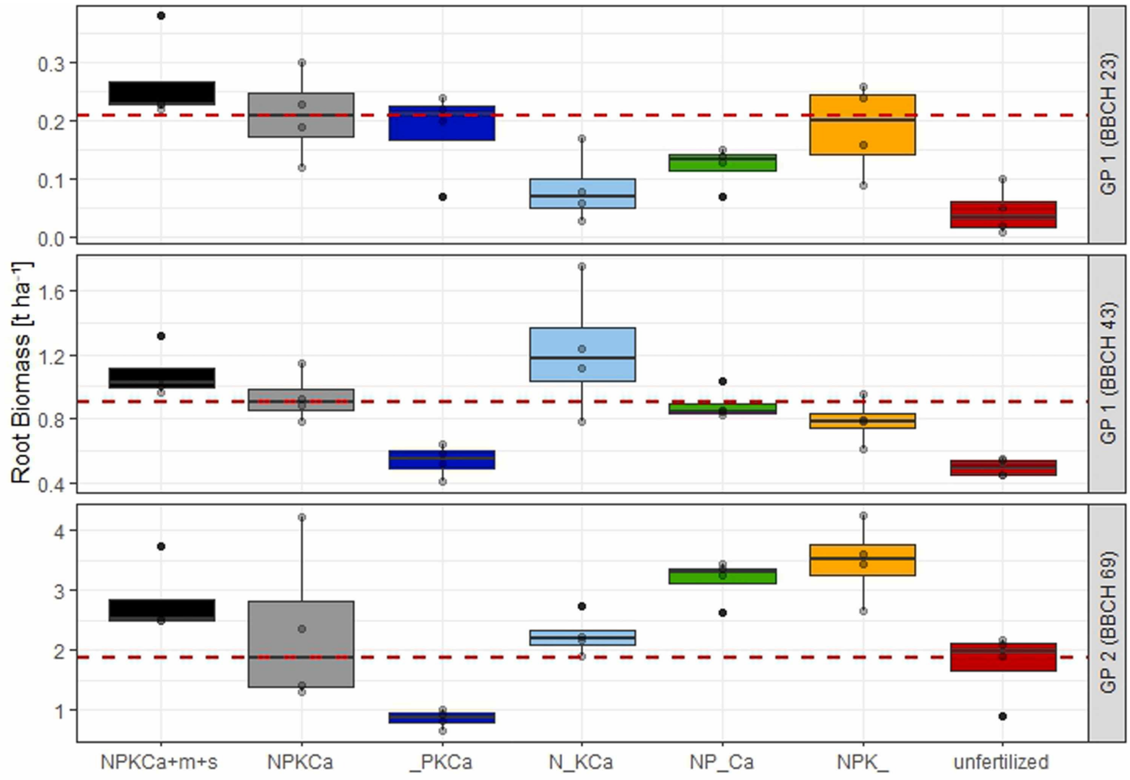

Figure 3.4: Total root biomass (t ha^{-1}) across different treatments during GP1: growing period 1 (2019/20 - BBCH 23), growing period 1 (2019/20 - BBCH 43) and GP2: growing period 2 (2020/21 - BBCH 69). The red dashed line represents the median root biomass of the NPKCa treatment as a baseline for comparison. Boxplots indicate the variability and median root biomass within each treatment.

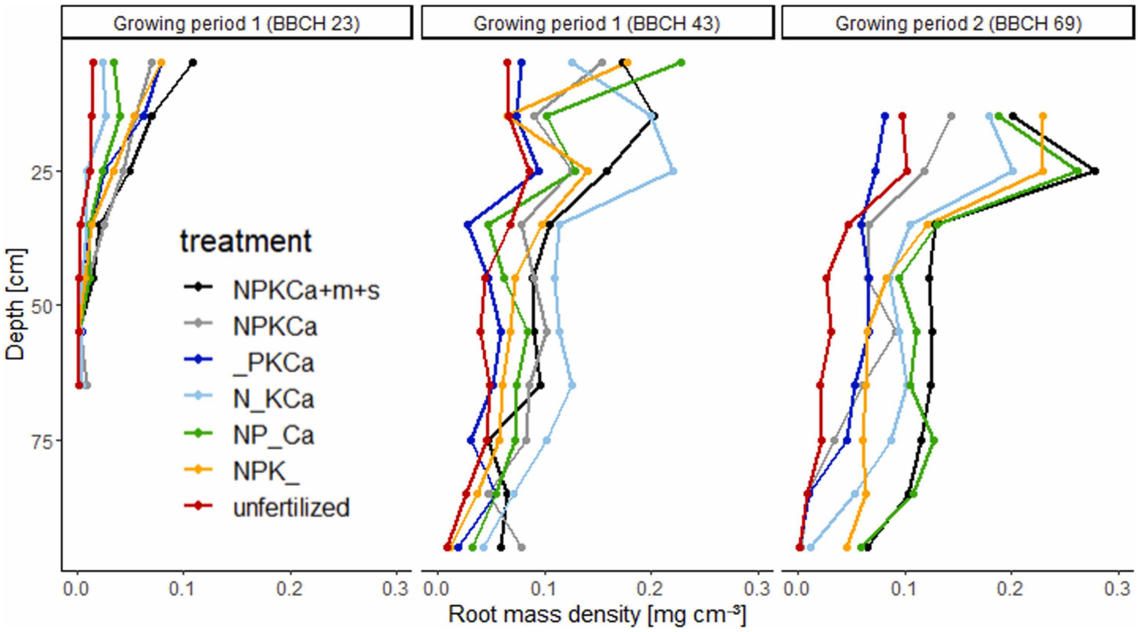

Figure 3.5: Observed mean (n=4) root mass density (mg cm^{-3}) in seven treatments of the LTFE Dikopshof, Germany for growing period 1 (2019/20 - BBCH 23), growing period 1 (2019/20 - BBCH 43) and growing period 2 (2020/21 - BBCH 69). The values of RMD of the first layer (0–10 cm) in growing period 2 (BBCH 69) were omitted to avoid distorting the graph and allow a comparison between treatments. However, the values can be observed in Table B.8 of the supplementary material. Standard deviation within each treatment is shown in SI in Tables B.6, B.7, and B.8.

Link analysis

At both sampling dates (BBCH 23 and 43) during growing period 1, the treatments _PKCa, N_KCa, NP_Ca, and unfertilized led to more external-external (EE) links in the topsoil roots than NPKCa (Fig. B.6a, B.6b in supplementary material). In the subsoil (60–70 cm depth) at BBCH 23, all treatments developed less EE links than NPKCa (Fig. B.6a and Table B.9). In contrast, at BBCH 43, the link types were similar among all treatments in the subsoil (80–90 cm) (Fig. B.6b and Table B.10). In growing period 2 (2020/21, BBCH 69), the proportion of EE, EI, and II links were similar among treatments in the topsoil (Fig. B.6c). However, in the subsoil, roots in treatments NPKCa, _PKCa, and the unfertilized treatment developed more EE links than the remaining treatments (Fig. B.6c and Table B.11).

3.3.2 Aboveground parameters

Shoot biomass, leaf area index, and plant height

Throughout growing periods 1 (2019/20) and 2 (2020/21), the NPKCa+m+s treatment exhibited greater shoot dry biomass, LAI, and plant height in comparison with the NPKCa treatment, as indicated in Table 3.3, Table 3.4. During growing period 1 (2019/20), the unfertilized and _PKCa treatments consistently yielded the lowest values on all sampling dates. On the other hand, NPKCa, N_KCa, NP_Ca, and NPK_ resulted in similar shoot dry matter, LAI, and plant height across most of the sampling dates in growing period 1 (2019/20) (see Table 3.3 and Table B.12).

In growing period 2 (2020/21) across all sampling dates, the NP_Ca, NPKCa+m+s, N_KCa, and NPK_ treatments exhibited higher values for shoot biomass and LAI than NPKCa treatment while the _PKCa and unfertilized treatments produced lower values for these traits in comparison with NPKCa (refer to Table 3.4).

Plants and ears per m^2

During growing period 1 (2019/20) at BBCH 23–28, the NPKCa treatment recorded the highest plant density, reaching 151 plants per m^2. In comparison, all the other treatments had lower densities (the lowest was the unfertilized treatment with only 54 plants per m^2). Conversely, in the second growing period (2020/21) at BBCH 69, the NPKCa treatment had one of the lowest plant densities, with only 251 plants per m^2. This was just above the _PKCa treatment (135 plants per m^2), and the unfertilized treatment (167 plants per m^2). The NPKCa+m+s treatment exhibited the highest plant and ear density. Detailed data on plant and ear counts for all treatments during both growing periods are presented in Table B.13.

In growing period 1 (2019/20), the unfertilized treatment consistently exhibited delayed growth, as indicated by retarded BBCH stages, in comparison to the other treatments. However, in growing period 2 (2020/21), both the _PKCa and unfertilized treatments inhibited the plant development, particularly during the tillering and early flowering stages.

Table 3.3: Observations of the mean phenological development stage (BBCH stage), shoot dry biomass, leaf area index (m^2 m^{-2}), and plant height (cm) of winter wheat cultivated in seven treatments of the LTFE Dikopshof, Germany, in growing period 1 (2019/20). Means with standard deviation within each treatment are presented. Some dates were excluded in this table but are shown in Table B.12 in the SI.

Samp. Date	**Treatment**	**BBCH**	**Dry biomass (t ha^{-1})**	**LAI (m^2 m^{-2})**	**Height (cm)**
17/03/20	NPKCa+m+s	23	0.25 ± 0.02	0.31 ± 0.03	6.2 ± 0.6
	NPKCa	23	0.23 ± 0.06	0.26 ± 0.06	5.3 ± 0.5
	_PKCa	23	0.16 ± 0.01	0.21 ± 0.02	5.1 ± 0.4
	N_KCa	23	0.18 ± 0.01	0.22 ± 0.01	4.6 ± 1.0
	NP_Ca	23	0.16 ± 0.03	0.19 ± 0.04	5.0 ± 0.5
	NPK_	23	0.17 ± 0.01	0.21 ± 0.01	6.2 ± 0.6
	unfertilized	23	0.07 ± 0.02	0.09 ± 0.03	5.0 ± 0.2
07/04/20	NPKCa+m+s	25	0.83 ± 0.11	0.99 ± 0.17	
	NPKCa	24	0.54 ± 0.08	0.56 ± 0.03	
	_PKCa	24	0.43 ± 0.03	0.44 ± 0.03	
	N_KCa	24	0.52 ± 0.04	0.54 ± 0.03	
	NP_Ca	24	0.58 ± 0.04	0.61 ± 0.05	
	NPK_	25	0.61 ± 0.12	0.59 ± 0.16	
	unfertilized	24	0.22 ± 0.08	0.21 ± 0.07	
22/04/20	NPKCa+m+s	31	1.86 ± 0.09	1.86 ± 0.14	20.7 ± 2.8
	NPKCa	31	1.16 ± 0.11	1.07 ± 0.12	14.5 ± 1.2
	_PKCa	31	0.86 ± 0.08	0.82 ± 0.07	11.5 ± 1.0
	N_KCa	31	1.29 ± 0.05	1.22 ± 0.06	13.2 ± 1.5
	NP_Ca	31	1.12 ± 0.15	1.08 ± 0.15	12.3 ± 1.8
	NPK_	31	1.14 ± 0.29	0.98 ± 0.26	14.9 ± 1.8
	unfertilized	31	0.45 ± 0.18	0.41 ± 0.16	9.2 ± 1.4
07/05/20	NPKCa+m+s	37	4.87 ± 0.36	3.89 ± 0.29	43.0 ± 4.0
	NPKCa	37	2.77 ± 0.37	1.84 ± 0.25	33.4 ± 0.3
	_PKCa	37	2.06 ± 0.12	1.35 ± 0.05	26.7 ± 1.3
	N_KCa	37	3.35 ± 0.45	2.17 ± 0.26	30.2 ± 2.5
	NP_Ca	37	2.89 ± 0.61	1.96 ± 0.49	31.7 ± 2.5
	NPK_	37	2.77 ± 0.31	1.72 ± 0.18	34.6 ± 1.1
	unfertilized	32	0.58 ± 0.21	0.34 ± 0.12	20.9 ± 1.8
19/05/20	NPKCa+m+s	43	5.11 ± 0.89	2.28 ± 0.36	54.1 ± 4.3
	NPKCa	43	4.40 ± 0.80	1.68 ± 0.25	45.5 ± 1.4
	_PKCa	43	3.51 ± 0.54	1.15 ± 0.21	36.8 ± 0.9
	N_KCa	45	4.83 ± 0.42	1.82 ± 0.11	45.5 ± 3.4
	NP_Ca	43	4.38 ± 0.81	1.72 ± 0.25	43.6 ± 1.1
	NPK_	43	4.91 ± 0.87	1.94 ± 0.31	48.7 ± 2.8
	unfertilized	39	1.91 ± 0.22	0.74 ± 0.05	35.4 ± 2.8

Table 3.4: Observations of the mean phenological development stage (BBCH stage), shoot dry biomass, leaf area index (m^2 m^{-2}), and plant height (m) of winter wheat cultivated at seven treatments at the LTFE Dikopshof, Germany, in growing period 2 (2020/21). Means with standard deviation within each treatment are presented.

Samp. Date	**Treatment**	**BBCH**	**Dry biomass (t ha^{-1})**	**LAI (m^2 m^{-2})**	**Height (cm)**
05/05/21	NPKCa+m+s	28	0.91 ± 0.11	0.85 ± 0.14	21.6 ± 1.9
	NPKCa	27	0.85 ± 0.27	0.85 ± 0.36	19.5 ± 1.4
	_PKCa	26	0.29 ± 0.06	0.30 ± 0.05	16.1 ± 0.4
	N_KCa	26	0.99 ± 0.15	0.91 ± 0.09	22.3 ± 0.7
	NP_Ca	25	1.24 ± 0.16	1.18 ± 0.14	25.5 ± 0.9
	NPK_	26	0.95 ± 0.09	0.86 ± 0.10	22.6 ± 0.7
	unfertilized	24	0.28 ± 0.07	0.23 ± 0.05	16.9 ± 0.8
08/06/21	NPKCa+m+s	59	5.08 ± 0.64	2.12 ± 0.22	73.6 ± 1.0
	NPKCa	58	4.27 ± 0.44	1.71 ± 0.12	72.1 ± 2.6
	_PKCa	57	1.04 ± 0.11	0.47 ± 0.03	49.6 ± 2.2
	N_KCa	57	5.11 ± 0.66	1.90 ± 0.30	69.1 ± 1.5
	NP_Ca	59	6.55 ± 0.68	2.27 ± 0.20	73.5 ± 1.5
	NPK_	59	5.77 ± 0.34	2.53 ± 0.17	71.6 ± 0.3
	unfertilized	58	0.77 ± 0.19	0.35 ± 0.07	44.4 ± 1.0
28/06/21	NPKCa+m+s	69	10.33 ± 0.78	1.82 ± 0.07	78.4 ± 1.1
	NPKCa	69	8.02 ± 1.10	1.35 ± 0.25	74.0 ± 1.4
	_PKCa	69	1.98 ± 0.16	0.32 ± 0.02	51.2 ± 1.1
	N_KCa	69	8.20 ± 0.45	1.32 ± 0.12	73.2 ± 1.2
	NP_Ca	69	11.89 ± 0.70	1.64 ± 0.10	75.2 ± 1.6
	NPK_	69	10.11 ± 0.83	1.50 ± 0.11	74.9 ± 1.0
	unfertilized	69	1.30 ± 0.24	0.21 ± 0.04	49.0 ± 3.5

Grain and straw yield

The omission of N and the absence of any fertilization resulted in a reduction in both straw and grain yield during both growing periods. Conversely, the straw and grain yield of the NPKCa, N_KCa, NP_Ca, and NPK_ treatments were similar between each other during either growing period. The NPKCa+m+s treatment exhibited particularly high grain yield, as well as straw yield, during both growing periods (as depicted in Fig. 3.6, Fig. 3.7 and Fig. B.7).

In the growing period 2 (2020/21), the mean grain yield exhibited an average reduction of 27% as compared to the growing period 1 (2019/20). However, the decline was more pronounced in the unfertilized and N_KCa treatments, with a reduction of 52% and 34%, respectively. NPK_ and NP_Ca treatments showed a relatively mild decline, with a reduction of 10% and 16%, respectively (Fig. 3.6). In contrast, the straw yield behaved differently, with most treatments showing an increase in the growing period 2 (2020/21) compared to the growing period 1 (2019/20). NPK_, NP_Ca, and NPKCa treatments showed an increase in straw yield (60%, 43%, and 43%, respectively), whereas N_KCa exhibited a slight increase of 5%. However, the _PKCa and unfertilized treatments were severely affected, showing a reduction of 81% and 75%, respectively (Fig. 3.7).

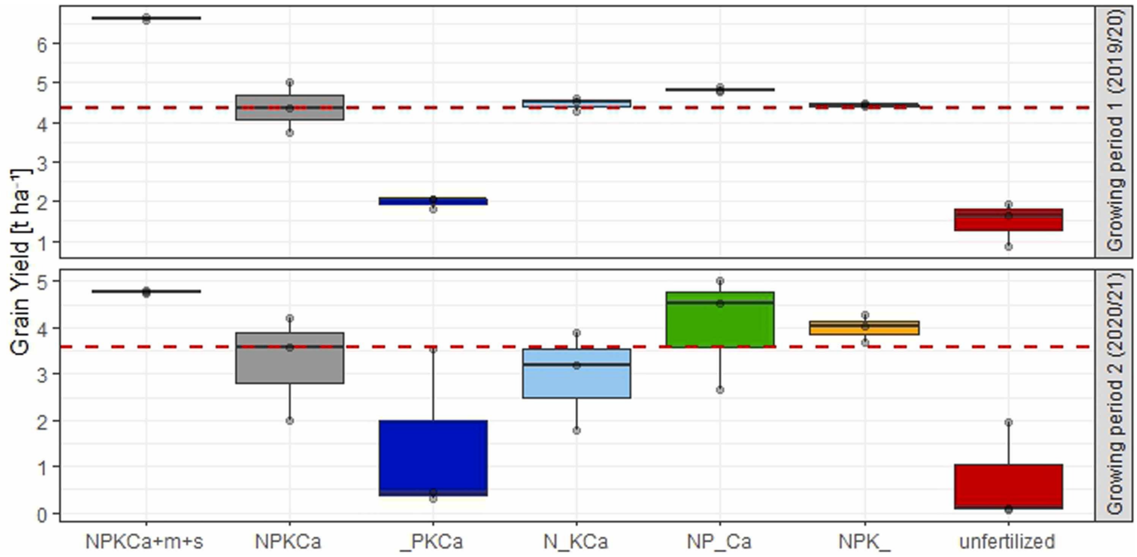

Figure 3.6: Observed dry matter grain yield of winter wheat cultivated in seven treatments of the LTFE Dikopshof, Germany during growing period 1 (2019/20) and growing period 2 (2020/21). The dashed red line represents the median of NPKCa treatment.

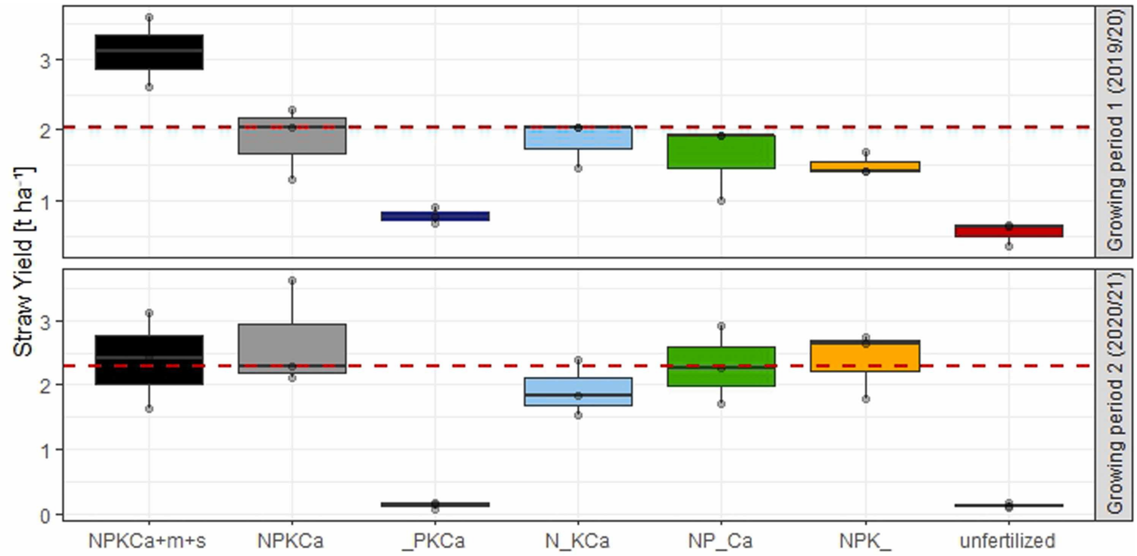

Figure 3.7: Observed dry matter straw yield of winter wheat cultivated in seven treatments of the LTFE Dikopshof, Germany during growing period 1 (2019/20) and growing period 2 (2020/21). The dashed red line represents the median of NPKCa treatment.

3.3.3 Performance-related ratios for above- and belowground traits: SLA, SRL, R/S and root length per shoot biomass

The performance-related ratios during the two root sampling dates in growing period 1 (2019/20 – BBCH 23 and BBCH 43) and the one root sampling date in growing period 2 (2020/21 -BBCH 69) are shown in Table 3.5.

Table 3.5: Specific leaf area (m^2 kg^{-1}), specific root length (m g^{-1}), root-to-shoot ratio and root length per shoot biomass (km kg^{-1}) during the two root sampling dates in growing period 1 (2019/20 – BBCH 23 and BBCH 43) and the one root sampling date in growing period 2 (2020/21 – BBCH 69). Means with standard deviation within each treatment are presented.

Period	**Treatment**	**Specific leaf area (m^2 kg^{-1})**	**Specific root length (m g^{-1})**	**Root-to-shoot ratio**	**Root length per shoot biomass (km kg^{-1})**
Growing period 1 (2019/20) Tillering	NPKCa+m+s	12.7 ± 0.20	124.5 ± 29.0	1.08 ± 0.30	130.4 ± 20.3
	NPKCa	11.7 ± 1.15	158.4 ± 56.6	0.93 ± 0.26	146.5 ± 27.0
	_PKCa	12.8 ± 0.36	119.1 ± 44.9	1.12 ± 0.49	134.7 ± 80.4
	N_KCa	12.2 ± 0.22	80.9 ± 20.1	0.46 ± 0.32	39.9 ± 32.2
	NP_Ca	12.4 ± 0.14	102.0 ± 44.4	0.79 ± 0.22	79.3 ± 35.1
	NPK_	12.1 ± 0.14	201.9 ± 61.1	1.09 ± 0.47	207.1 ± 61.1
	unfertilized	11.4 ± 0.77	304.3 ± 177.1	0.68 ± 0.74	177.2 ± 85.0
Growing period 1 (2019/20) Booting	NPKCa+m+s	12.5 ± 0.61	198.3 ± 15.7	0.21 ± 0.02	42.7 ± 7.7
	NPKCa	10.8 ± 0.37	172.1 ± 12.2	0.21 ± 0.03	36.9 ± 5.4
	_PKCa	9.1 ± 0.29	273.6 ± 98.1	0.16 ± 0.06	39.8 ± 5.7
	N_KCa	10.6 ± 0.39	177.5 ± 26.5	0.26 ± 0.10	45.3 ± 16.7
	NP_Ca	11.1 ± 1.03	214.4 ± 25.1	0.21 ± 0.04	44.8 ± 13.0
	NPK_	11.1 ± 0.42	212.1 ± 37.4	0.16 ± 0.02	33.9 ± 5.4
	unfertilized	10.8 ± 0.78	248.8 ± 35.4	0.26 ± 0.06	66.2 ± 19.4
Growing period 2 (2020/21) Flowering	NPKCa+m+s	11.1 ± 1.46	91.2 ± 13.1	0.28 ± 0.07	24.5 ± 2.9
	NPKCa	12.9 ± 1.16	52.8 ± 19.1	0.28 ± 0.13	13.2 ± 3.4
	_PKCa	9.7 ± 0.71	90.1 ± 21.3	0.44 ± 0.10	38.2 ± 3.2
	N_KCa	10.8 ± 0.51	78.2 ± 20.6	0.28 ± 0.13	20.9 ± 1.9
	NP_Ca	8.3 ± 1.22	72.6 ± 12.4	0.27 ± 0.04	19.5 ± 3.1
	NPK_	8.3 ± 1.55	50.4 ± 6.7	0.35 ± 0.09	17.2 ± 1.9
	unfertilized	8.9 ± 0.88	40.7 ± 17.2	1.36 ± 0.41	50.4 ± 4.7

3.3.4 Relative changes of traits and indices under nutrient deficiency compared to full fertilization

The relative change of shoot and root traits across different treatments with NPKCa as the baseline (Fig. 3.8) showed that the NPKCa+m+s treatment consistently enhances most parameters such as grain and straw yield, shoot and root biomass, root length, SLA, SRL, and root length per shoot biomass. The R/S was similar to the baseline. Additionally, N deficiency and unfertilized conditions reduce grain and straw yield, root and shoot biomass, and root length but increased SRL, R/S, and root length per shoot biomass, with some exceptions. Furthermore, P and K deficiencies as well as the omission of liming reduced straw yield but increased root length and the root length per shoot biomass, with some exceptions.

	Growing Period	BBCH	NPKCa+m+s	_PKCa	N_KCa	NP_Ca	NPK_	unfertilized
Grain yield (t ha^{-1})	1 (2019/20)	89	↑ 51%	↓ -55%	→ 2%	↑ 10%	→ 1%	↓ -66%
	2 (2020/21)	89	↑ 46%	↓ -56%	↓ -9%	↑ 25%	↑ 22%	↓ -78%
Straw yield (t ha^{-1})	1 (2019/20)	89	↑ 65%	↓ -58%	→ -2%	↓ -14%	↓ -20%	↓ -70%
	2 (2020/21)	89	↓ -11%	↓ -95%	↓ -28%	↓ -14%	↓ -10%	↓ -95%
Shoot biomass (t ha^{-1})	1 (2019/20)	23	↑ 9%	↓ -27%	↓ -20%	↓ -31%	↓ -23%	↓ -67%
	1 (2019/20)	43	↑ 16%	↓ -20%	↑ 10%	→ 0%	↑ 12%	↓ -56%
	2 (2020/21)	69	↑ 29%	↓ -75%	→ 2%	↑ 48%	↑ 26%	↓ -84%
Total root biomass (t ha^{-1})	1 (2019/20)	23	↑ 26%	↓ -13%	↓ -60%	↓ -42%	↓ -11%	↓ -79%
	1 (2019/20)	43	↑ 16%	↓ -42%	↑ 31%	↓ -5%	↓ -16%	↓ -47%
	2 (2020/21)	69	↑ 21%	↓ -63%	→ -3%	↑ 36%	↑ 50%	↓ -24%
Total root length (m)	1 (2019/20)	23	→ 1%	↓ -30%	↓ -77%	↓ -59%	↑ 11%	↓ -62%
	1 (2019/20)	43	↑ 34%	↓ -12%	↑ 36%	↑ 18%	→ 3%	↓ -23%
	2 (2020/21)	69	↑ 142%	↓ -28%	↑ 65%	↑ 122%	↑ 66%	↓ -38%
Specific leaf area (m^2 kg^{-1})	1 (2019/20)	23	↑ 8%	↑ 9%	→ 4%	↑ 6%	→ 3%	→ -2%
	1 (2019/20)	43	↑ 16%	↓ -15%	→ -2%	→ 3%	→ 3%	→ 1%
	2 (2020/21)	69	↓ -13%	↓ -25%	↓ -16%	↓ -36%	↓ -35%	↓ -31%
Specific root length (m g^{-1})	1 (2019/20)	23	↓ -21%	↓ -25%	↓ -49%	↓ -36%	↑ 27%	↑ 92%
	1 (2019/20)	43	↑ 15%	↑ 59%	→ 3%	↑ 25%	↑ 23%	↑ 45%
	2 (2020/21)	69	↑ 73%	↑ 71%	↑ 48%	↑ 37%	→ -5%	↓ -23%
Root-to-shoot ratio	1 (2019/20)	23	↑ 16%	↑ 20%	↓ -50%	↓ -15%	↑ 18%	↓ -27%
	1 (2019/20)	43	→ 0%	↓ -26%	↑ 20%	→ -3%	↓ -25%	↑ 23%
	2 (2020/21)	69	→ -3%	↑ 56%	→ -1%	↓ -5%	↑ 24%	↑ 378%
Root length per shoot biomass (km kg^{-1})	1 (2019/20)	23	↓ -11%	↓ -8%	↓ -73%	↓ -46%	↑ 41%	↑ 21%
	1 (2019/20)	43	↑ 16%	↑ 8%	↑ 23%	↑ 21%	↓ -8%	↑ 79%
	2 (2020/21)	69	↑ 85%	↑ 188%	↑ 58%	↑ 47%	↑ 30%	↑ 280%

Figure 3.8: Relative change of shoot and root trait across different treatments. The baseline for the analysis is the values of NPKCa treatment. Green arrows indicate higher values, yellow arrows represent similar values (from -5 to 5%), and red arrows denote lower values. Comparisons were made between treatments within the same growing period and BBCH.

3.3.5 Correlation of traits

Data used in Pearson correlation is included in Table B.14. In the entire profile, LAI and shoot biomass consistently showed a moderate positive correlation with C_{org}, total soil N_t, and N_{min} at all sampling dates. Root biomass consistently exhibited a moderate positive correlation with LAI and shoot biomass in both growing periods and all BBCH stages. Root length consistently displayed a positive moderate correlation with root biomass in all three sampling dates in both growing periods (Fig. 3.9).

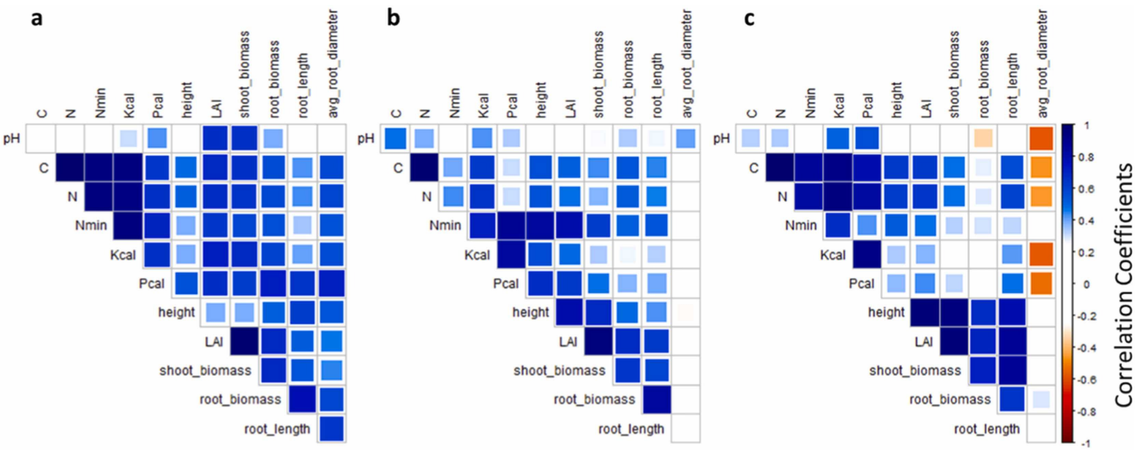

Figure 3.9: Pearson correlation for soil properties, above- and belowground traits during the shoot-root sampling dates: a) First sampling date in growing period 1 (2019/20, BBCH=23), b) Second sampling date in growing period 1 (2019/20, BBCH=43), and, c) First sampling date in growing period 2 (2020/21, BBCH=69). P-values between -0.3 to 0.3 are not significant.

Additionally, during growing period 1 (2019/20) at BBCH 23, LAI and shoot biomass displayed a moderate positive correlation with soil pH, K_{cal}, and P_{cal} (which is not observed in growing period 2). Average root diameter displayed a moderate positive correlation with soil nutrients, root length and root biomass (Fig. 3.9a). However, in the same growing period at BBCH 43, average root showed no significant correlation with the other analyzed parameters (Fig. 3.9b). In growing period 2 (2020/21) at BBCH 69, the average root diameter displayed a moderate negative correlation with soil pH, C_{org}, total soil N_t, K_{cal}, and P_{cal} (Fig. 3.9c).

Across all sampling dates, there are strong positive correlations between C_{org}, N_t, N_{min}, K_{cal}, and P_{cal} in both the topsoil and subsoil (Fig. B.8 and Fig. B.9). Aboveground traits such as height, LAI, and shoot biomass correlate strongly with each other. Belowground traits (root traits) generally show positive correlations with shoot traits.

In the topsoil (Fig. B.8), LAI, shoot, and root biomass were positively correlated with soil nutrients during growing period 1 (2019/20 - BBCH 23), particularly with P_{cal}. Furthermore, N_{min} was positively correlated with LAI, shoot biomass, root biomass, and root length during growing period 1 (2019/20 - BBCH 43). Average root diameter exhibited a strong negative correlation with other traits in growing period 2 (2020/21 - BBCH 69).

In the subsoil (Fig. B.9), specifically, N_{min} positively correlates with LAI and shoot biomass during growing period 1 (BBCH 43). Furthermore, C_{org} and N_t positively correlate with plant height, LAI, shoot and root biomass, and root length during growing period 2 (2020/21 - BBCH 69).

3.3.6 PCA analysis

The PCA analysis was conducted to highlight the variability among treatments based on key shoot and root variables. The scree plot (Fig. B.10 in SI) shows that the first two principal components (PC1 and PC2) account for a combined 67.2% of the total variance, with PC1 explaining 47.2% and PC2 20%.

PC1 primarily separates treatments based on variables such as root biomass, shoot biomass, LAI, and plant height, with positive associations along the positive PC1 axis (Fig. 3.10). PC2 captures secondary variability, driven by traits such as SLA and root length.

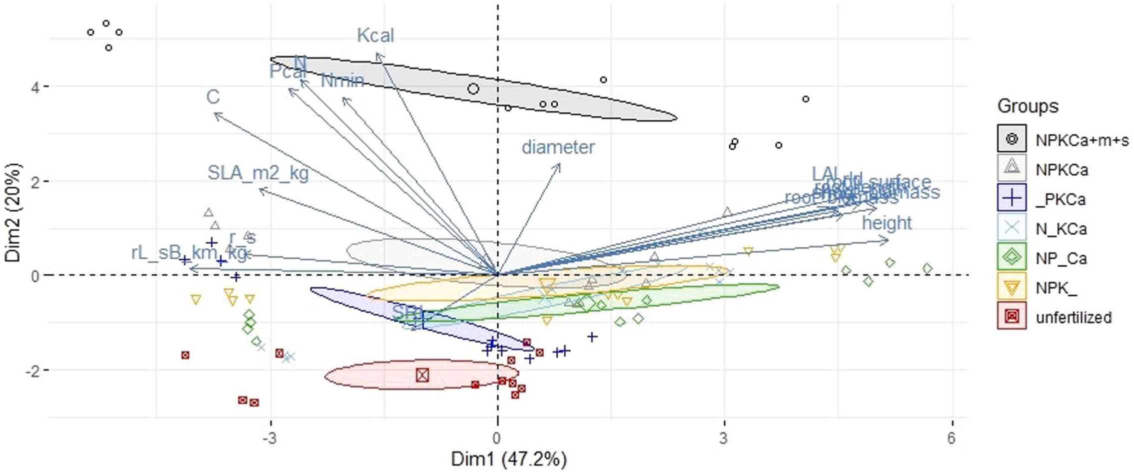

Figure 3.10: PCA biplot illustrating the relationships between trait variables (arrows) and treatments (symbols) across the first two principal components (Dim1=PC1 and Dim2=PC2). The arrows represent the contributions of variables, with their direction and length indicating the strength and influence on the principal components. Treatments are plotted based on their scores along PC1 and PC2, showing the variability and separation of responses to different treatments.

The treatments exhibited distinct responses in growth performance. The NPKCa+m+s treatment formed a separate cluster with positive associations on PC1 and PC2, indicating increased root and shoot biomass (Fig. 3.10). In contrast, the unfertilized treatment aligned negatively with PC1, reflecting poor performance across the analyzed traits. The NPK_ and NP_Ca treatments overlapped, suggesting similar moderate responses. Other treatments, such as NPKCa, N_KCa and _PKCa, varied along PC1 and PC2 based on their specific trait contributions.

3.4 Discussion

The aim of this study was to investigate the response of above- and belowground traits to nutrient deficiencies and evaluate the performance of the crop under nutrient-poor conditions. Specifically, we examined aboveground traits such as shoot biomass, LAI, and plant height, as well as belowground traits including root biomass, total root length, RLD, and various ratios that provide insights into plant performance.

We expected to observe a decrease in shoot biomass, LAI, root biomass, and root length under nutrient deficiencies while anticipating an increase in the examined ratios as indicators of nutrient stress. Some of our results align with previous studies and support these expectations.

3.4.1 Belowground traits and their responses to soil nutrients

As expected, total root biomass and length were highest in the most nutrient-rich treatment (NPKCa+m+s) and lowest in treatments with low nutrient availability, particularly under severe N deficiency (_PKCa) and in the unfertilized treatment. This decline aligns with findings that nutrient deficiencies reduce root growth due to limited resource availability for cell division and elongation (Giehl and von Wirén, 2014).

While severe N deficiency negatively impacted absolute root biomass, root length (especially in the subsoil), and RLD in our study, previous research has shown that mild N deficiency can stimulate root growth as plants increase their nutrient foraging efforts (Comfort et al., 1988; Jia and von Wirén, 2020; NaNagara et al., 1976; Peng et al., 2012). This discrepancy could be attributed to varying degrees of N limitation severity. The studies reporting enhanced root growth generally investigated moderate N limitations and focused on early growth stages, during which plants may exhibit compensatory root growth. In contrast, severe N deficiency, especially in later growth stages, typically reduces root biomass and length due to insufficient resources for cell division and elongation. For example, Lopez et al. (2023) reported in a meta-analysis a mean decrease in root length and biomass (about 18%) under N deficiency.

Further, P deficiency can stimulate lateral root growth and fine root development (Liu, 2021; Zhang et al., 2012) as a compensatory mechanism to enhance P acquisition by increasing root surface area in contact with the soil (Bonifas and Lindquist, 2009; Williamson et al., 2001). This effect was observed in our study, where P omission resulted in similar or greater root biomass and length compared with the NPKCa treatment during booting and flowering. This adaptive response, regulated by hormone signaling involving auxin and ethylene (Hermans et al., 2006), may provide an advantage in nutrient-deprived conditions by promoting root foraging into the topsoil and subsoil. Similar root elongation and biomass increases under P deficiency have been reported in common bean (Lynch, 2011), though contrasting findings in wheat indicate root length and biomass reductions (Teng et al., 2013).

As for the effect of K deficiency on winter wheat root traits, the lack of field studies limits our ability to draw definitive conclusions. Nevertheless, a decrease in root length in K-poor soils has been observed in studies with cotton (Mullins et al., 1994), maize (Zhao et al., 2016), and sugar beet (Hadir et al., 2020). Our findings show that K deficiency lowered root biomass only at an early stage (tillering) but increased root length at booting and flowering. This variability highlights the complexity of root responses to K deficiency based on the genotype and soil conditions (Rengel and Damon, 2008) and may show that root length increases at later stages as a compensatory response.

While the root biomass in NPK_ was slightly lower than in the NPKCa treatment, root length was similar or greater. This may suggest that a slightly reduced pH, as observed in our experiment, facilitates the mobilization of certain cations such as iron, zinc, and manganese. These micronutrients are essential for root metabolic processes and cell elongation, potentially supporting root growth. This phenomenon was demonstrated in a previous experiment conducted at the same site (LTFE Dikopshof), where sugar beet leaves treated with NPK_ displayed an increase in zinc and nickel content (Yi et al., 2020).

Regarding other investigated root traits, such as the link analysis, the literature suggests that root systems grown in low nutrient conditions tend to have longer link lengths, particularly interior (II and EI) links. This distinguishes them from classic herringbone root systems where branching is predominantly confined to a main axis, typically found in dicots with tap roots. Herringbone-type root systems are generally more efficient in acquiring mobile nutrients such as N or K, although they are more costly for the crop in terms of production and maintenance (Fitter and Stickland, 1991; Hadir et al., 2020). In line with the result of Fitter and Stickland (1991) who observed that dicots exhibited the tendency described above while monocots did not, our experiment involving winter wheat, a monocot plant, did not show large differences.

3.4.2 Aboveground traits

The grain yield during the growing period 2 (2020/21) was lower compared to the growing period 1 (2019/20), despite experiencing higher total precipitation. This could be attributed to the contrasting weather patterns between 2020 and 2021. In 2020, although it was warmer overall, there were significant rainfalls in February/-March and June. On the other hand, in 2021, there was low rainfall from March to May, and even though it was colder in general, the temperature in June (during flowering) was quite high. These differences in temperature and rainfall patterns likely influenced the grain yield. In contrast, the straw yield was lower in the growing period 1 (2019/20), which could be attributed to the prevailing drought conditions. The lower harvest index in 2021, as well as the high mean air temperatures in June (Fig. S1), indicate heat and drought stress during flowering, which has a significant impact on winter wheat yield (Yu et al., 2018).

The treatment with the highest soil nutrient content (NPKCa+m+s) consistently exhibited greater aboveground traits, including shoot dry biomass, LAI, and plant height, while the unfertilized and _PKCa treatments consistently yielded the lowest values across all sampling dates. This aligns with studies showing that nutrient deficiencies, particularly N deficiency, significantly reduce grain and straw yields due to its essential role in chlorophyll formation, photosynthesis, and protein synthesis (Fageria, 2009; Hermans et al., 2006; Qin et al., 2018). Overall, fertilizer omission led to declines in grain yield, straw yield, and shoot biomass, as nutrient limitations restrict the availability of essential elements required for photosynthesis and biomass production, ultimately reducing yield (Liu et al., 2020b).

Furthermore, N_KCa treatment resulted in similar shoot dry matter, LAI, and plant height in comparison with NPKCa, with no severe decrease observed. This suggests that the omission of P may not be critical for the development of shoot biomass on this site with a relatively nutrient-rich soil, which is supported by previous research on long-term data (various crops) under P fertilizer omission (Deubel et al., 2002; Gransee and Merbach, 2000; Kunzová and Hejcman, 2010; Seidel et al., 2021; Zicker et al., 2018). These findings indicate that the impact of P deficiencies on wheat shoot biomass may be relatively small.

In our study, K omission led to an increase in grain yield but a decrease in straw yield compared with full fertilizer treatment, which contrasts with other research showing that K deficiency generally reduces both grain and straw yields due to its crucial role in carbohydrate metabolism and transport (Brhane et al., 2017; Pettigrew, 2008). Shoot biomass, LAI, and plant heights in K omission were similar (to NPKCa) in one period but greater in another, potentially due to very low shoot performance in NPKCa in the latter year. Typically, K is crucial for activating enzymes involved in photosynthesis and for the translocation of photosynthates from source to tissues (Tränkner et al., 2018). Its deficiency harms these processes, leading to inhibited growth and reduced biomass (Hasanuzzaman et al., 2018). Additionally, K regulates stomatal opening and closing, which controls water use efficiency and drought tolerance. K deficiency often results in poor water regulation, contributing to reduced plant vigor (Perez et al., 2016; Schroeder and Hagiwara, 1990).

In our study, the total shoot biomass in NPK_ was similar to NPKCa, which is consistent with the study of Ahrends et al. (2020), who analyzed long-term yield data from four crops in the LTFE. They reported similar mean yields for the NPKCa and NPK_ treatments, with a slight decline observed in the NPK_ treatment (e.g., winter wheat yield of 4.7 t ha^{-1} for NPKCa vs. 4.51 t ha^{-1} for NPK_). While Ca is generally not limiting, the absence of additional lime application in NPK_ could contribute to competitive interactions among base cations (e.g., Mg, K) or other indirect effects on nutrient availability and uptake.

3.4.3 Performance-related ratios for above- and belowground traits

Some studies suggest that lower SLA, indicating thicker leaves, may be a response to reduced water loss under nutrient stress (Poorter et al., 2009). However, our findings did not show substantial changes in SLA under N deficiency, suggesting that other adaptive mechanisms may be involved. Similarly, we did not observe a consistent trend in SLA under K deficiency. Environmental conditions, particularly in the growing period 1 (2019/20), which was warmer and drier with limited rainfall even during typically wetter months like July, may have influenced plant responses. This could explain why SLA under K deficiency was greater than that of the NPKCa treatment early during this period. However, at BBCH 43, SLA was comparable to the NPKCa treatment. Some studies have also reported no significant changes in SLA under moderate K deficiency (Pettigrew, 2008; Zhang et al., 2020a). In contrast, severe nutrient stress, as seen in unfertilized treatments, can sometimes alter SLA, but this varies with the severity of the deficiency and plant adaptation strategies (Xu and Mou, 2016). In our study, SLA under unfertilized conditions was similar to NPKCa in 2019/20 but lower in 2020/21.

While SLA responses to nutrient deficiencies varied, root system adaptations provided further insights into plant strategies for coping with limited nutrient availability. Our study showed that N deficiency and unfertilized conditions led to increases in SRL, R/S, and root length per shoot biomass, indicating a shift in resource allocation towards root development to enhance nutrient acquisition. Higher SRL suggests the development of finer roots, which are more efficient in nutrient uptake, while increased R/S and root length per shoot biomass reflect an strategy to optimize nutrient acquisition under stress (Hermans et al., 2006). In contrast, no consistent pattern was observed for SRL and R/S under P deficiency, though previous research suggests that wheat plants often respond by increasing R/S to enhance P uptake efficiency (de Souza Campos et al., 2019). Similarly, increased root length per shoot biomass under P deficiency indicates a strategic allocation of resources toward root development to enhance nutrient uptake while ensuring reproductive success (Junaidi et al., 2018; Lopez et al., 2023).

Beyond N and P deficiencies, root responses to K and Ca omissions revealed distinct adaptation patterns. K deficiency in our study resulted in a decrease in R/S, contrasting with studies reporting an increase as plants prioritize root growth to explore more soil for nutrients (Andrews et al., 1999). In the Ca omission treatment, SRL, R/S, and root length per shoot biomass generally increased, enhancing nutrient uptake efficiency by expanding the root surface area and optimizing resource allocation (Eissenstat, 1992).

3.4.4 Correlation of traits

Our findings show relationships between plant traits and soil nutrient dynamics. LAI and shoot biomass were moderately correlated with C_{org}, N_t, and N_{min} across all sampling dates, consistent with studies linking nutrient availability to biomass production and soil carbon inputs (Ziter and MacDougall, 2013). Root biomass correlated with LAI and shoot biomass, reflecting its role in plant growth and yield (Bektas et al., 2023; Shamuyarira et al., 2022). Similarly, root length and root biomass were consistently correlated, though root length is more sensitive to environmental and management changes and is closely linked to aboveground biomass (Ma et al., 2019). Aboveground traits such as height, LAI, and shoot biomass showed strong correlations, as reported by Gleason et al. (2018). Positive correlations between above- and belowground traits, including root biomass and root length with shoot biomass, align with studies on shoot-root biomass allocation influenced by species traits and growth stages (Bektas et al., 2023; Husáková et al., 2018; Mokany and Ash, 2008).

3.4.5 Other insights of our study

Roots contribute to soil C_{org} through root turnover, exudation, and decomposition of dead roots (Tresder et al., 2005). Under optimal nutrient conditions (e.g., NPKCa+m+s), increased root biomass may enhance carbon inputs, improving soil structure, fertility, and overall health. Conversely, nutrient deficiencies (e.g., N, P, K, Ca) reduce root biomass, leading to lower carbon inputs and potentially affecting C_{org} levels and soil quality (Rasse et al., 2005). Fine roots, which decompose more rapidly than coarse roots, play a crucial role in carbon cycling. The observed increase in fine roots under P deficiency in our study suggests a potentially higher contribution to C_{org} despite overall reductions in root biomass, as fine roots release carbon into the soil more efficiently (Gill and Jackson, 2000). The ability of plants to allocate resources to root growth, particularly under nutrient stress, indicates an adaptive strategy to maintain nutrient uptake efficiency and contribute to soil carbon dynamics. This adaptation can be crucial for long-term soil health and fertility, as continuous root inputs are vital for sustaining C_{org} levels (Wang et al., 2023, 2024c).

In this regard, Long-term experiments (LTEs) are important in agricultural research, particularly for studying root dynamics and soil–plant interactions under varying nutrient levels while maintaining the same climate and soil type (Grosse et al., 2021; Körschens, 2021). The LTE at Dikopshof has provided valuable insights into the long-term effects of nutrient management on shoot development and now on root growth. LTEs allow us to observe how plants evolve over multiple growing seasons, providing a comprehensive understanding of shoot and root dynamics. Nutrient application, soil changes, and crop rotation practices can have cumulative effects on soil properties and root development. These LTEs, such as Dikopshof (which has the same fertilizer management over decades), help in understanding how these cumulative effects influence root growth and function over time, offering a more holistic view of plant–soil interactions. By covering multiple years, LTEs give an understanding of varying weather conditions, and other environmental factors. This variability is key to understanding the resilience and adaptability of root systems under different climatic scenarios. These insights are essential for developing sustainable agricultural practices that optimize root growth and nutrient uptake while maintaining soil health (Grosse et al., 2021; Körschens, 2021). However, one limitation of the Dikopshof LTE is the absence of spatial replicates for its treatments, which complicates the application of standard statistical analyses, particularly for short-term studies. Despite this limitation, the advantages of an LTE, including long-term data collection and insights into plant–soil dynamics, make it invaluable for understanding the effects of treatments over time.

Our findings drew a picture of the complex interactions between nutrient deficiencies and shoot and root performance. The variations in response observed in different treatments highlight the importance of considering above- and belowground traits and environmental conditions when evaluating nutrient stress. Further research is justified to explore the mechanisms driving these responses and to elucidate the potential implications for crop productivity and nutrient management strategies.

3.5 Summary and conclusions

This study aimed to investigate above- and belowground trait responses to nutrient deficiencies and crop performance under nutrient-poor conditions. As expected, shoot and root biomass decreased under nutrient deficiencies, while the treatment with the highest nutrient content consistently exhibited superior aboveground traits. In contrast, unfertilized and low-nutrient treatments showed the lowest values. Weather patterns, particularly drought, likely influenced lower grain yield in the growing period 2 (2020/21). Absolute root biomass and length increased with fertile soils, while reductions under P and K deficiencies were primarily observed at early growth stage. Soil pH reductions had varied effects on root traits. Unexpected trends in above- and belowground trait ratios may be linked to resource competition. These findings highlight the complex interactions between nutrient availability, plant performance, and environmental factors, underscoring the need for further research on crop productivity and nutrient management strategies. Future studies should explore cultivar-specific responses and incorporate higher temporal resolution sampling for a more detailed analysis.

Chapter 4

Root:Shoot ratio of field crops under conventional and conservation tillage: A meta analysis

This chapter has been published as:
Ahmadi, S. H., Seidel, S. J., Lopez, G., Kamali, B., Gaiser, T., Hadir, S., Demie, D. T., Andersen, M. N., Ewert, F., & Ochoa, I. H. (2024). Root:Shoot ratio of field crops under conventional and conservation tillage: A meta analysis. *Soil Use and Management*, 41(1), e70026. `https://doi.org/10.1111/sum.70026`

Abstract

Conventional tillage (CT) is a widely used agricultural practice aimed at loosening soil to enhance water infiltration and root growth. However, it can lead to environmental issues such as increased soil erosion and loss of nutrients and carbon. To address these challenges, non-conventional tillage systems like no-tillage and minimum tillage (collectively referred to as NT) have gained popularity in recent decades. This review examines the effects of CT and NT on the root:shoot ratio (R:S) based on 28 studies covering common crops across various climates and managements. Most studies were primarily on maize, wheat, rapeseed and barley. Meta-analysis showed non-significant differences ($p = .27$) among these crops with respect to their response of R:S to the two tillage practices. Rapeseed and barley exhibited higher R:S in NT by 2% and 15%, while maize and wheat demonstrated higher R:S in CT by 2% and 6%, respectively, although the effects were not significant. In terms of soil texture classes, crops grown in sandy soils had a higher R:S under CT than NT, but no significant differences were found ($p = .19$). However, significant differences emerged among soil textures, with silty clay, sandy loam and clay loam showing the highest R:S ($p < .05$) while a cluster of sandy clay loam, clay and loam had lower R:S. Additionally, dicot crops displayed an 8% higher R:S under NT compared with CT, although this was not statistically significant ($p = .24$). Results indicated no significant differences ($p = .22$) in R:S between deep ($> 30\,\mathrm{cm}$) and shallow ($< 30\,\mathrm{cm}$) root sampling depths. The findings indicate that more field experiments are needed to fully understand the impact of tillage methods on R:S across genotypes, environments and managements.

4.1 Introduction

Soil tillage is a primary agricultural activity in arable crop production (Thomas et al., 2007; Topa et al., 2021). Tillage operations primary aim is to loosen compacted soil, enhance porosity and lower topsoil bulk density to create an optimal seedbed (Kuhn et al., 2016; Mohammadi et al., 2024; Tian et al., 2023). Tillage impacts soil properties like moisture, aeration, temperature and penetration resistance, which in turn influence crop growth. It also promotes root development and soil health by increasing root-derived soil organic carbon content (Buyanovsky and Wagner, 1996; Cooper et al., 2021; Hou et al., 2018; Izaurralde et al., 2007; Jin et al., 2007; Kuhn et al., 2016; Kuzyakov, 2002; Mu et al., 2014; Peixoto et al., 2020; Seidel et al., 2022).

There is a global trend toward shifting from conventional tillage (CT) systems, like deep ploughing, to conservation tillage methods, including minimum tillage and no-tillage (NT) (Devkota et al., 2022; Ma et al., 2024). These methods are increasingly used in crop rotations to reduce soil organic matter loss and prevent topsoil degradation (de Moraes Sá et al., 2014; He et al., 2009; Kuhn et al., 2016; Mehra et al., 2018; Mondal et al., 2019). Daryanto et al. (2020) argue, however, that NT alone is insufficient and should be integrated with cover crops to improve environmental benefits. Compared with CT, NT generally increases soil water content and bulk density (Devkota et al., 2022; Kuhn et al., 2016; Munkholm et al., 2013; Muñoz-Romero et al., 2012; Soane et al., 2012), though long-term NT may reduce topsoil bulk density and enhance soil conditions by improving aggregation, pore size distribution and organic matter content (Bessam and Mrabet, 2003; Carter, 1992; Galdos et al., 2019; Jemai et al., 2013; Li et al., 2007; Mohammadi et al., 2024; Tian et al., 2023).

Several studies have shown that the impact of tillage on root growth is site- and crop-specific, yielding contrasting findings (Blanco-Canqui and Ruis, 2018; Lal, 1985; Merrill et al., 1996; Schneider et al., 2017; Wilhelm, 1998). Soil properties such as moisture, bulk density, temperature and nitrogen fertilizer application influence root growth patterns and stratification under no-tillage (NT) compared with conventional tillage (CT) (Hou et al., 2018; Muñoz-Romero et al., 2010b,a; Officer et al., 2009; Plaza-Bonilla et al., 2014). For instance, Seidel et al. (2022) found higher root length densities in spring barley and winter wheat with deep loosening compared with untreated soil. Conversely, Hobson et al. (2022) reported no significant difference in root mass between NT and CT in winter wheat in a 60 cm loamy sand profile. Du et al. (2024) noted that NT increased root length and mass of rainfed spring wheat to 50 cm in loess soil, while Guan et al. (2015) found CT increased root length and mass of rainfed winter wheat to 110 cm in light loam, enhancing water use efficiency because of lower soil bulk density and penetration resistance. This is supported by findings from Zhou et al. (2021), Zhang et al. (2020b), Atkinson et al. (2020), Hodgkinson et al. (2017), and Andersen et al. (2013). Similarly, Plaza-Bonilla et al. (2014) found no significant difference in winter wheat root mass between CT and NT down to 90 cm across various silty soils, while Sidiras et al. (2001) reported higher root mass in NT for winter barley in the top 30 cm. These conflicting results highlight the difficulty in determining the definitive effects of tillage systems on root growth (Zhao et al., 2023). However, some studies suggest that NT may support continuous macropores for root growth (Ehlers et al., 1980; Galdos et al., 2019; Kay and VandenBygaart, 2002; Kuhn et al., 2016; Tian et al., 2023; Wardak et al., 2022; Zhou et al., 2021).

The root:shoot ratio (R:S) is a complex trait that varies among crops and their varieties in response to environmental conditions (Bolinder et al., 1997; Mokany et al., 2006). It serves as an essential ecological index for evaluating plant health and its effects on crop yield and production (Agathokleous et al., 2019; Osaki et al., 1996). Understanding R:S and root mass allocation is vital for insights into carbon allocation and storage in ecosystems (Bolinder et al., 1997; Mokany et al., 2006), agricultural soils (Heinemann et al., 2023), soil carbon sequestration (Heinemann et al., 2023; Kätterer et al., 2012), crop production (Bolinder et al., 2007; Huck et al., 1986) and nutrient uptake (Bacher et al., 2022; Lynch et al., 2012). The R:S ratio fluctuates throughout the growing season (Bolinder et al., 2002, 2007; Lynch et al., 2012) and is influenced by environmental factors (water, nutrients, CO_2), agricultural practices (tillage type and depth, machinery traffic) and genotypes (Anderson, 1988; Fang et al., 2017; Heinemann et al., 2023; Lynch et al., 2012; Meurer et al., 2018; Redin et al., 2018; Wasson et al., 2014). Therefore, studying R:S is crucial for assessing the physiological status of cropping systems (Lopez et al., 2023; Mokany et al., 2006).

Comprehensive literature reviews have explored the effects of water stress (Foxx and Fort, 2019; Kou et al., 2022), CO_2 levels (Madhu and Hatfield, 2013; Rogers et al., 1995) and nutrient deficiencies (Lopez et al., 2023) on the R:S. Additionally, reviews focusing on the impacts of various tillage systems on soil properties (Liu et al., 2021; Mathew et al., 2017; Shaheb et al., 2021), crop growth and yield (Achankeng and Cornelis, 2023; Schneider et al., 2017; Zhao et al., 2023), soil nutrients (Lopez et al., 2023; Topa et al., 2021), soil carbon pools (Mehra et al., 2018; Mondal and Chakraborty, 2022) and environmental quality (Shakoor et al., 2021; Xiao et al., 2020) have also been conducted. However, no focused review exists on how tillage systems specifically influence R:S.

This study aims to fill this gap by investigating the effects of tillage systems on root and shoot coordination (R:S) under field conditions. While many field experiments focus primarily on crop yield or environmental effects related to tillage systems (Busari et al., 2015; Toliver et al., 2012), this study does not concentrate on the impacts of tillage systems on crop yield, soil nutrients or carbon pools, as previous studies have extensively covered these aspects (Du et al., 2022; Holland, 2004; Morris et al., 2010; Schneider et al., 2017; Young et al., 2021). Therefore, the objectives of this study are twofold: (1) to review the reported R:S ratios for common field crops across varied environmental conditions and (2) to assess how soil texture and crop type interact with tillage systems to influence R:S. This study will quantify the effects of CT and NT on R:S, comparing the relative R:S of CT to NT, with CT serving as the reference point.

4.2 Data and statistics

This review aims to compare the effects of CT and NT on the R:S, defined as the dry weight of root mass (R) divided by the dry weight of shoot mass (S). To estimate the effects of tillage on R:S, we calculated the relative R:S under conventional tillage (R:S_{CT}) divided by R:S under non-conventional tillage (R:S_{NT}) including tillage systems like no-tillage, zero tillage and minimum tillage as (R:S_{CT}/R:S_{NT}).

We collected the data reported in the literature to investigate the effects of CT and NT practices on R:S ratios. Data exploration was performed using Google Scholar, Web of Science, Scopus and the search engines of the publishers (Elsevier, Springer, Taylor and Francis and Wiley). To search for the relevant literature, the combination of keywords included 'root, shoot, root shoot, root:shoot, root/shoot, shoot:root, shoot/root, root to shoot, shoot to root, aboveground, belowground, tillage, no-tillage, zero tillage, conventional tillage, conservative tillage, tilled, no tilled' and excluded 'grass, grassland, cover crop, pot, controlled conditions'. The literature references in the manuscripts were also checked for any paper that we might have missed in our search.

The emphasis of this review is on field crops grown under field conditions. Experiments done under controlled conditions (greenhouse or climate chambers), as well as pot experiments were excluded from the analysis because of the pot size effect on shoot and root growth (Kiær et al., 2013; NeSmith and Duval, 1998; Poorter et al., 2012; Wheeldon et al., 2021). Poorter et al. (2012) demonstrated that pot size can significantly influence R:S, with smaller pots potentially skewing experimental results. NeSmith and Duval (1998) suggested that container size alters the rooting volume available to plants, significantly affecting growth. Other studies have shown pot volume strongly impacts shoot growth (Hess and De Kroon, 2007; McConnaughay and Bazzaz, 1991). Moreover, Kiær et al. (2013) reported that limited root volume in small pots can lead to a higher R:S because of increased competition among roots for resources, resulting in greater root mass and reduced shoot mass. We also skipped the papers on subsoiling. One major criterion was that the root and shoot samples were collected at the same time at the anthesis or at harvest where roots are fully extended.

The R:S data was either explicitly stated in the paper, or we calculated it based on the reported values of root and shoot mass. The extracted data from each publication was either tabulated or summarized in bar plots or line plots. The root sampling depth varied in different studies (Figure 4.1). The sampled roots and harvested shoots in the experimental fields were oven-dried to obtain the dry mass of root and shoot. Roots are collected either by soil coring sampling or by excavation sampling using shovels in different studies (Ahmadi et al., 2020; Trachsel et al., 2013). The R:S ratios were calculated by dividing root dry mass to the shoot dry mass. The WebPlotDigitizer, version 5.3 (Burda et al., 2017; Rohatgi, 2017) was used to extract the exact values of the data when displayed in plot style.

In total, 196 papers that satisfied the search criteria were retrieved, but after screening for suitability of data quality and quantity, only 28 papers remained for further analyses. Most of the collected data was on maize (39 datapoints), followed by wheat (26), barley (22) and rapeseed (11). Overall, 117 pairs of R:S observations

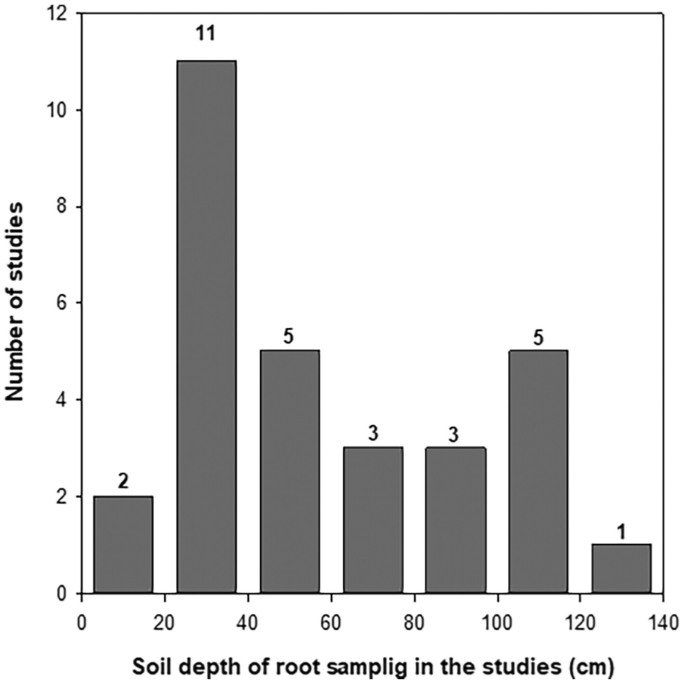

Figure 4.1: Histogram of the soil sampling depth in different studies for determining root biomass. The numbers above each bar indicate the number of studies with the reported root sampling depths.

(234 datapoints) for 12 different field crops were identified. The major limitation of the study is that the data and available field studies are too limited that causes more uncertainties. However, this study generally provides a comprehensive result though with limitations. This indicates that more specific studies are required to study the effect of diverse tillage systems on the root-to-shoot coordination.

For the statistical analysis, the t-test analysis assuming unequal variances was employed to compare the means of two groups based on the Shapiro–Wilk test for normality. In case of two mean comparisons when the data of each group were not normally distributed, we used the non-parametric Mann–Whitney U-test. When comparing more than two means, the non-parametric Kruskal–Wallis H-test was used (McCarroll, 2016; Mendenhall and Sincich, 2016). All the statistical analysis were done in the R environment (version 4.4.1). The mean ± standard deviation (SD) has also been calculated for the inferential statistics. In case, higher SD than mean indicates the data is highly dispersed or spread out relative to its mean and are from different sources as in the meta-analyses.

4.3 Results and discussion

4.3.1 General effects of tillage-induced bulk density on root:shoot ratio

The logarithmic scatter plot of the R:S in the NT and CT systems are illustrated in Figure 4.2. Overall, the majority of the R:S values were below 0.6. The large variation of R:S in different studies suggests a strong interaction of crop type, soil, climate conditions and management (Heinemann et al., 2023). In addition, the effect of variety and genotype might have played a significant role in the large differences of R:S among crops (Hamedani et al., 2020; Mathew et al., 2019), which may imply the high influence of crop type over soil type of region. Our findings are in line with the estimates of R:S for small grain cereals at the highest standing biomass ranging from 0.09 to 0.63 under conventional system (Bolinder et al., 2007; Buyanovsky and Wagner, 1986; Paustian et al., 1990). However, extreme values of R:S may also be found for some crops up to 2.5 (Figure 4.2). For instance, for barley some datapoints are extremely high and close to 2. The same is the case for wheat with two datapoints close to 1 but many datapoints are below 0.1. Wheat has shown a wide range of variation in R:S. Several studies have also confirmed a wider variation of R:S in wheat and reported very high R:S in wheat genotypes up to 1.13 (Fang et al., 2017), 3.04 (Mathew et al., 2017), and 4.1 (Narayanan et al., 2014). However, it could be likely that the extreme values might be because of root confinement in a compacted soil layer (Batey, 2009; Hamza and Anderson, 2005).

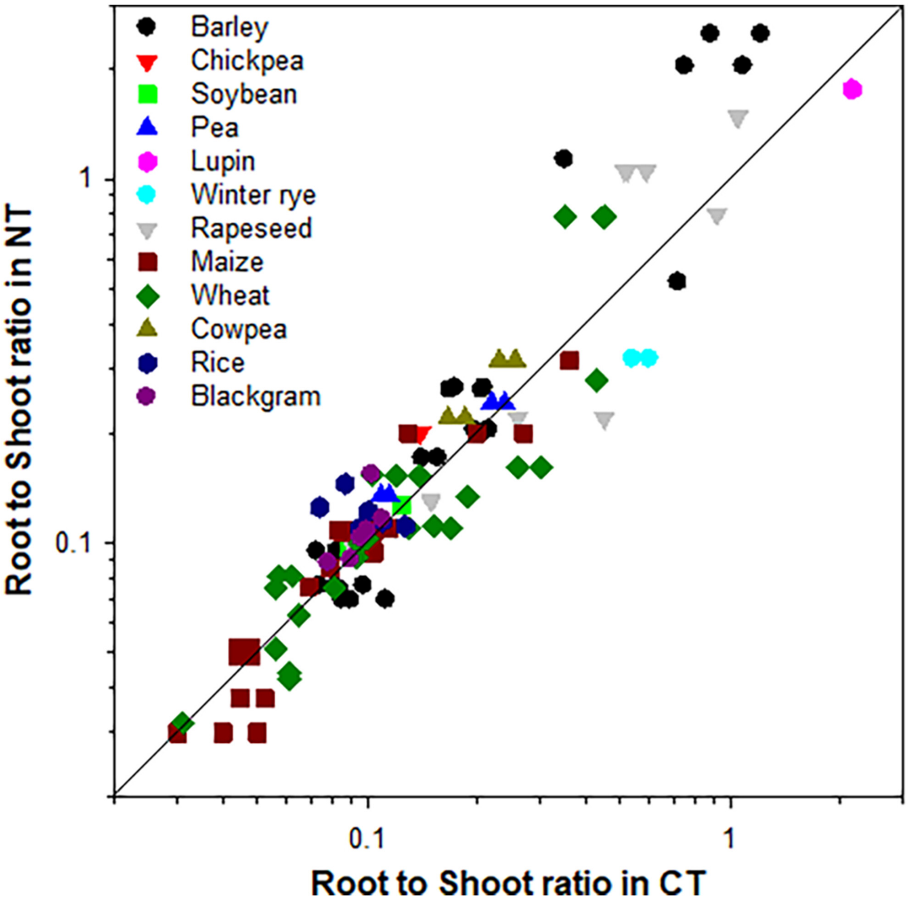

Figure 4.2: Logarithmic scatter plot of the root to shoot ratios in the conservation (NT) and conventional tillage (CT) systems. The solid line is the 1:1 line.

Among the four crops with the highest number of datapoints, the R:S of maize varied between 0.03 and 0.4 (Figure 4.2). This range of variations of R:S is also reported in other studies for maize (Benjamin et al., 2014; Heinemann et al., 2023). The R:S of rapeseed varied between 0.08 and 1, a wider range than maize. In this regard, Heinemann et al. (2023) argued that winter wheat exhibited a wide variety of R:S, both across different study sites and within the same site. In contrast, silage maize genotypes displayed a consistent root-to-shoot ratio. This indicates that certain crops may be more advantageous than others for increasing root biomass while still achieving desired yield levels. For crops with fixed R:S, like maize, breeding efforts may be less effective compared with those aimed at enhancing root biomass in more adaptable crops such as winter wheat. Although the findings are somewhat constrained by limited data, a range of potential variabilities was identified, highlighting the knowledge gap that hampers both theoretical predictions and the practical application of optimized genotype selection.

Averaged over all data in Figure 4.2, the R:S in NT and CT were 0.29 ± 0.48 and 0.22 ± 0.29 (mean ± SD), although they were not significantly different ($p = .19$). It is well established that tillage practices would affect root growth and its coordination with shoot growth through changing soil bulk density (Lopez et al., 2023; Panagos et al., 2024; Toth et al., 2024). Although several studies have reported that NT increases the soil bulk density (Chen et al., 1998; Ehlers et al., 1983; Logsdon and Karlen, 2004; Nunes et al., 2015), there is ample literature with contrasting findings about an increase in soil bulk density (e.g. Singh et al., 2016), a decrease (e.g. Gathala et al., 2011) and no change (e.g. Mondal et al., 2018) under NT. Many inter-related factors such as soil texture, organic matter, water content and penetration resistance may influence soil bulk density in the NT that are rarely discussed in the literature (Daryanto et al., 2020; Farahani et al., 2022; Fengyun et al., 2011). Therefore, the change in soil bulk density because of applying NT does not necessarily reduce root mass as it is already reported for wheat (Huang et al., 2012), oats (Ehlers et al., 1980, 1983), and maize (Himmelbauer et al., 2012). Moreover, a meta-analysis conducted by Mondal et al. (2020), reported that NT increases root mass in the topsoil layer (0–20 cm) were because of the greater availability of water and nutrients. However, Lampurlanés and Cantero-Martínez (2003) reported that although NT resulted in higher soil bulk density than CT, barley root growth improved in a well-structured soil because roots could grow between the soil aggregates, continuous cracks and biopores (old root channels). Improved soil aggregate stability (higher mean-weight diameter) under NT is also reported by Hobson et al. (2022), Cooper et al. (2021), Galdos et al. (2019) and Martínez et al. (2008).

In addition, Toth et al. (2024), Nawaz et al. (2024), Godwin (1990) and Hill and Cruse (1985) reported that increasing soil bulk density up to a critical bulk density may not negatively impact root growth. Therefore, under certain soil, climate and management conditions (Martínez et al., 2008), soil bulk density under NT practices may not be high enough to reach this critical value and impose an appreciable inhibitory effect on root growth (Correa et al., 2019; Plaza-Bonilla et al., 2014). Such a non-limiting soil bulk density under NT has also been explicitly argued by Unger and Fulton (1990) and Jones (1983). Unger and Fulton (1990) reported favourable wheat and sorghum yields under NT, indicating that NT did not adversely affect any of the measured soil physical conditions including soil bulk density to the point that crop yields were adversely affected. In this regard, Dexter (2004) argued that root growth is effectively controlled by soil structure and micropores (soil moisture characteristic curve) rather than the soil bulk density. In line with this argument, Ahmadi et al. (2011) found the highest amount of root in the deep layers of a loamy sand with high bulk density (1.62 g cm^{-3}) and reported that bulk density was not acting as a sole limiting factor for root growth but other soil physical factors, such as soil structure, could be a better indicator for root growth. Therefore, it could be suggested that soil structure in terms of macropores, micropores and porosity plays a superior role on the influence of tillage systems (CT and NT) on root growth than soil bulk density itself (Galdos et al., 2019; Hobson et al., 2022). A well-structured soil irrespective of the non-limiting soil bulk density might be the major driver of root mass distribution in the soil (Perkons et al., 2014; Topa et al., 2021; Wardak et al., 2024). This argument is also confirmed by Gao et al. (2016) who suggested that deep rooting under high soil bulk density is mostly related to the interaction between root system architecture and soil structure (macropores network) than is to the ability of a root to deform strong soil. Although the ability of roots to deform strong soil layer is a critical trait, Gao et al. (2016) stated that it is more related to root exploration of the surface soil layers than deep rooting. However, Nawaz et al. (2024) argued that root proliferation to deep soil layers under NT may also partly depend on the different plant roots characteristics relevant to penetration into the soil.

4.3.2 Effect of soil texture on R:S under CT and NT

The R:S data was analysed regarding the effects of main soil textures (Figure 4.3). Based on the limited data, the soils were then classified into three soil textural classes and the subclasses: Clay (sandy clay, silty clay and clay), Sand (loamy sand and sand) and Silt/Loam (sandy clay loam, silty clay loam, clay loam, silt, silt loam, loam and sandy loam) (Figure 4.4) according to the USDA soil particle size classification (USDA, 2017). Table C.1 shows the mean R:S in CT and NT and the corresponding relative R:S per each soil texture class and subclasses.

Statistical analyses revealed that the relative R:S of the three soil textural classes (clay, sand and silt/loam) were not significantly different (p = .35) (Table C.1). However, results suggest that soil texture has a great impact on the relative R:S such that in sandy soils R:S$_{\mathrm{CT}}$ is increased by 8% (relative R:S = 1.08) while in clayey soils it is decreased by 16% (relative R:S = 0.84) (Table C.1). This implies that NT in sandy soils tends to produce higher R:S, which could be generalized for the coarse soil textures (relative R:S > 1) compared with the fine soil textures (relative R:S < 1). Further analysis on comparing more than two means showed that soil textures silty clay, sandy loam and clay loam clustered in one group (not significant within group) had the highest relative R:S and were significantly ($p < .05$) different from the cluster of sandy clay loam, clay and loam in another group (not significant within group) with the lowest relative R:S. This is in line with the argument of Wardak et al. (2024) and Morris et al. (2017) that soil classes and tillage systems such as NT impact the structural integrity of soil, which in turn governs root growth and proliferation in the soil matrix.

The contrasting findings among soil textures might support the argument of Jones (1983) that percentage silt + clay is a better indicator of root growth than clay content alone. The review study of Schneider et al. (2017) has also highlighted the importance of the percentage of the silt and clay (clay > 20% and silt < 70%)

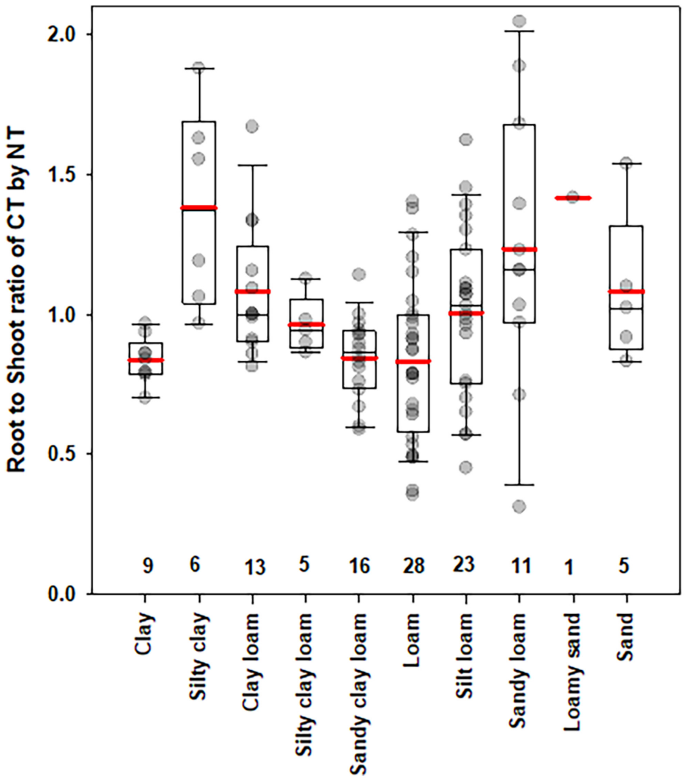

Figure 4.3: Box plot distribution of the relative root to shoot ratio under the CT and NT tillage systems (R:S$_{CT}$/R:S$_{NT}$) according to the major soil texture classes. The red line is the mean. The values below each box are the number of data points.

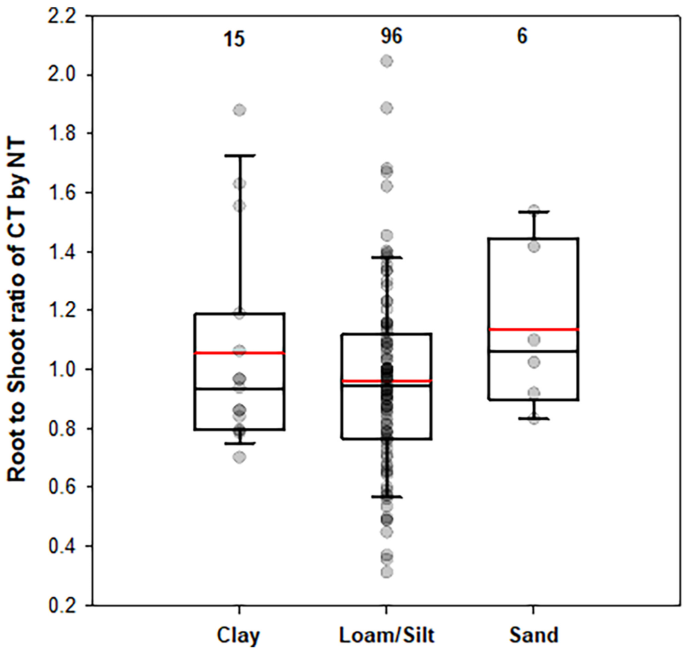

Figure 4.4: Collation and box plot distribution of the relative root to shoot ratio under the CT and NT tillage systems (R:S$_{CT}$/R:S$_{NT}$) according to the three major soil classes. The red line is the mean. The values above each box are the number of data points.

on root growth and soil structure, which indicates loamy and medium texture soils benefited more from NT than CT regarding improved soil structure and root growth. In addition, there are also studies that have reported the particular influence of clay content on root growth (Correa et al., 2019). Probert et al. (1987) and Muñoz-Romero et al. (2010b) reported that the effect of CT and NT on root mass and proliferation is negligible in clayey soils because of strong cohesion of soil particles and small pore sizes. Root growth ceases in clayey and sandy soils at bulk densities of 1.47 and 1.85 g cm^{-3}, respectively (Jin et al., 2017; Jones, 1983; Pierce et al., 1983), which shows soil bulk density at which root growth is halted depends on soil texture (Pierce et al., 1983; Toth et al., 2024; Unger and Kaspar, 1994).

Figure 4.4 shows that the majority of the studies have been done in loamy soil textures and R:S showed highly diverse and contrasting responses to tillage practices. Our analysis (Figures 4.3 and 4.4) suggests that soil texture classes play a less central role in R:S regulation such that, within the same soil texture class, NT and CT could have different effects on root and shoot growth. Soil physical properties other than soil texture such as water content, porosity and continuity of biopores, temperature and penetration resistance seem to be the main factors that may result in diverse relative R:S values within the same soil texture class (Martínez et al., 2008; Nawaz et al., 2024). In addition, other environmental and management factors like precipitation (Plaza-Bonilla et al., 2014) and the duration of NT over years (Bessam and Mrabet, 2003; Hill and Cruse, 1985; Li et al., 2007; Mondal and Chakraborty, 2022; Tian et al., 2023) could have also led to different responses of the R:S ratio to tillage systems within the same soil texture class. Several researchers have concluded that the most consistent results concerning NT on significant changes in soil structural properties, soil porosity and organic matter are obtained when measurements are made at or above 10 years after NT implementation (Cooper et al., 2021; Díaz-Zorita et al., 2004; He et al., 2009; Hobson et al., 2022; Kay and VandenBygaart, 2002; Lal et al., 1994). However, such long-term studies on the effect of NT on the topsoil properties are rare (Galdos et al., 2019; Xiao et al., 2020).

Several studies have shown that the effect of soil texture on R:S under different tillage systems would diminish when there is enough water in the soils for crop growth (Morell et al., 2011; Muñoz-Romero et al., 2010b,a; Plaza-Bonilla et al., 2014). Therefore, it is clear that observed variations of the R:S in the literature (Figures 4.3 and 4.4) could also be affected by the soil water content in each study (Jones, 1983). It is worth mentioning that soil nutrients (N, P and K) in different studies and soil textures and its interaction with soil water content could have influenced the R:S (Anderson, 1988; Huang et al., 2012; Lopez et al., 2023; Morell et al., 2011; Muñoz-Romero et al., 2010b,a; Poorter and Nagel, 2000).

4.3.3 Effect of crop type on R:S under CT and NT

Tillage systems have variable effects on R:S depending on crop types (Figure 4.2) (Bolinder et al., 2007). Figure 4.5 shows the variations of the relative R:S for the four major crops with the most available data for analysis. The mean values of the relative R:S are 0.87, 1.02, 1.06 and 0.98 for barley, maize, wheat and rapeseed, respectively. This shows that R:S$_{\mathrm{NT}}$ increased by 15% and 2% in barley and rapeseed compared with R:S_{CT}. However, in wheat and maize, R:S_{CT} increased by 2% and 6% compared with R:S_{NT}. This implies that barley has been the most responsive crop to NT. However, analysis of variance revealed that relative R:S values were not significant ($p = .27$) among these four crops.

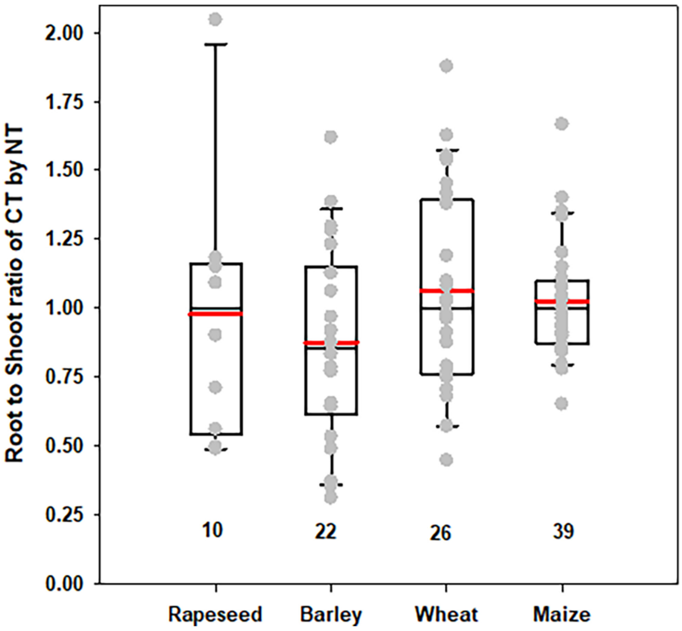

Figure 4.5: The box plot distribution of the relative root to shoot ratio data under the CT and NT tillage systems (R:S_{CT}/R:S_{NT}) for the four major crops with the most available data in the literature. The red line is the mean. The values below each box are the number of data points.

Furthermore, to narrow down our analysis, we split the crops into two categories as monocotyledonous (monocot) and dicotyledonous (dicot) annual crops. Figure 4.6 depicts the variations of the relative R:S in the monocots and dicots. The average of relative R:S in dicots (0.92) is lower than in monocots (1.00) though they are not significantly different ($p = .24$). Dicots showed a tendency to produce 8% higher R:S_{NT} (i.e. more roots or less shoot biomass) than R:S_{CT}. These results are in agreement with Schneider et al. (2017) who argued that the monocots and dicots have different abilities of root growth in the soil. Dicots have generally thicker roots and higher ability to grow into deeper depths and can branch at high soil resistance than monocots (Clark and Barraclough, 1999; Kautz et al., 2013). However, the cereals (monocots) have thin and fibrous roots, which may limit their ability to grow into deeper soil layers or layers with higher penetration resistance except under certain conditions that may allow deeper growth (Ahmadi et al., 2020; Schneider et al., 2017; Seidel et al., 2022), though Perkons et al. (2014) showed that barley has thicker roots than wheat and can potentially grow deeper down to 2 m in a well-structured soil. Presumably, monocots have a higher tendency to accumulate more root mass in the topsoil layers (Fan et al., 2016) and higher fractions of the roots are sampled for the monocots than the dicots under NT. An explanation could be because monocots have more difficulties to cope with the relatively unfavourable conditions in the topsoil of NT (more compact), thus they respond by allocating more resources in root growth in the topsoil layer (Thorup-Kristensen, 2001). Clark and Barraclough (1999) also confirmed that roots of dicots most often grow better in strong soil than monocots because the dicots generate greater root growth pressures. Therefore, it is concluded that the dicots have a more conservative response to tillage compared with monocots.

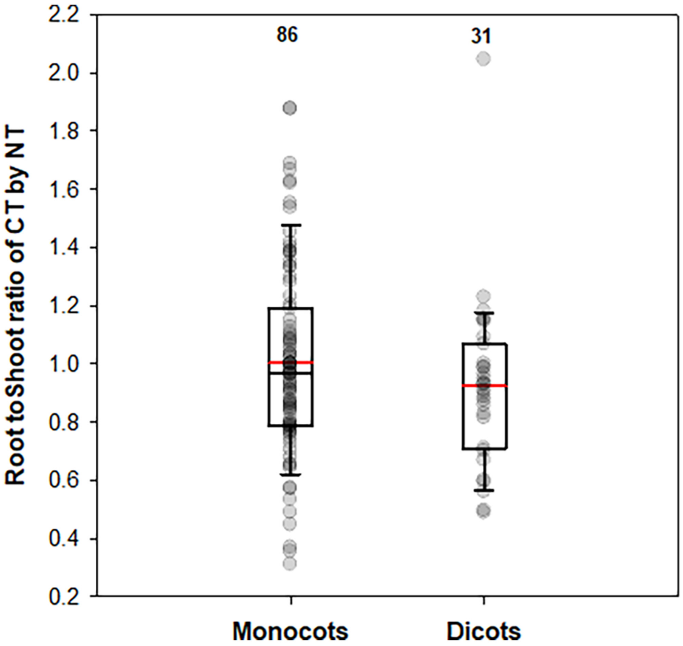

Figure 4.6: The box plot distribution of the relative root to shoot ratio data under the CT and NT tillage systems (R:S$_{\mathrm{CT}}$/R:S$_{\mathrm{NT}}$) for the two major crop species of monocots and dicots. The red line is the mean. The values above each box is the number of data points.

Sampling date and thus the crop rooting depth as well as the root sampling depth may influence R:S. The diverse studies in the literature have sampled roots from different soil depths (Figure 4.1) assuming that the majority of roots was sampled and collected contributed to root mass (Ahmadi et al., 2017, 2020; Fan et al., 2016). Our data analysis showed that there was not a significant difference ($p = .22$) between the means of R:S of the deep (>30 cm) and shallow (plough layer) (<30 cm) root sampling depths (Figure 4.7), which implies that the majority of the root mass has been sampled. According to Fan et al. (2016), 50% of the total root mass of maize, wheat, barley and rapeseed was found at the depths of, respectively, 14.4, 16.8, 11.5 and 8.4 cm from the soil surface, which shows that a high amount of root mass could be collected by sampling the topsoil layers. In another study, based on the root mass data from different soil depths, Hu et al. (2018) reported that 80% of the total root mass of cereals is allocated to the top 30 cm soil depth.

4.3.4 Further causes of variations of root and shoot components

Root and shoot mass, key components of the R:S, respond differently to tillage systems. Over the past 40 years, many studies have examined the effects of CT and

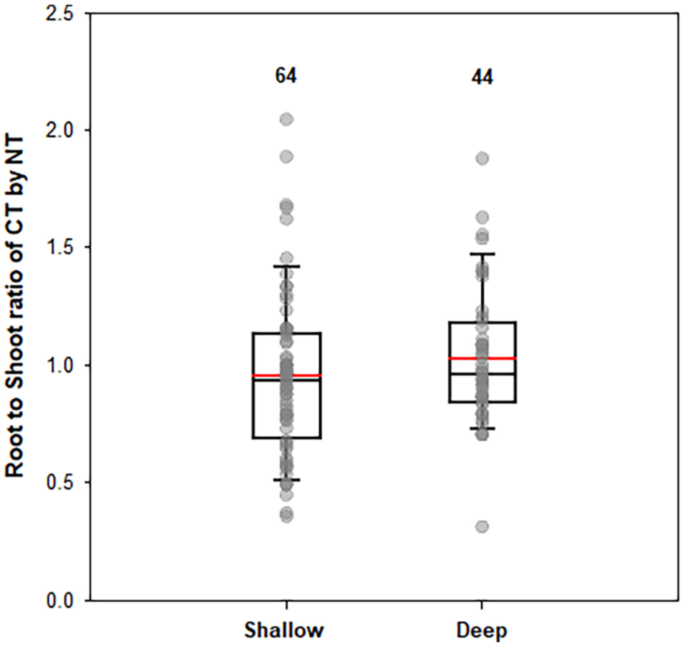

Figure 4.7: The box plot distribution of the relative root-to-shoot ratio data under the CT and NT tillage systems (R:S_{CT}/R:S_{NT}) for the two shallow (<30 cm) and deep (>30 cm) root sampling. The red line is the mean. The values above each box are the number of data points.

NT on crop yield (shoot) and root growth (Alvarez and Steinbach, 2009; Muñoz-Romero et al., 2010b,a). These studies indicate that the impact of tillage on yield and root traits varies by crop type (Vetsch et al., 2007), crop rotation interactions (Calonego and Rosolem, 2010; Pedersen and Lauer, 2003; Qin et al., 2004; Ribera et al., 2004), field management practices like sowing date (Sainju and Singh, 2001), cultivar (Popp et al., 2002), fertilizer application (Halvorson et al., 2000), tillage system type (You et al., 2017), duration of CT and NT (Pearson et al., 1991; Qin et al., 2004), as well as site-specific factors such as soil type, rainfall distribution (Muñoz-Romero et al., 2010b; Popp et al., 2002) and yearly climatic conditions (Calonego and Rosolem, 2010; Halvorson et al., 2000; Hou et al., 2018; Muñoz-Romero et al., 2011; Pedersen and Lauer, 2003; Qin et al., 2004).

There are several sources of uncertainty that may lead to large variations of R:S and therefore it is not possible to assign one R:S ratio to a crop species. One source of uncertainty is that root sampling depth differed in the reported studies (Figure 4.1), which has also been pointed out in earlier studies (Bolinder et al., 2007). Although there are uncertainties in the reported root mass in different studies, it seems that a large proportion of the root mass was retrieved in the soil samples according to the root mass distribution in the upper soil depth (Ahmadi et al., 2017, 2020; Fan et al., 2016; Hu et al., 2018; Schenk, 2008). The R:S variations within a crop species might be also partly explained by the sampling strategies and the root washing methods used in the studies (Amato and Pardo, 1994; Bolinder et al., 1997; Hadir et al., 2025; Noordwijk et al., 1985). Hirte et al. (2017) reported that maize root mass can be wrongly overestimated by 40% because of inclusion of organic matter such as old roots from previous studies or weed roots. Other factors such as fertilization and climatic variations probably contribute to the variability of R:S. Moreover, the root mass does not only vary among species, but may also vary among cultivars (Bolinder et al., 1997; Xu and Juma, 1993). Altogether, it is obvious that a precise but also a standardized procedure of root mass determination is very crucial for a reliable R:S ratio.

There are several studies with contrasting results regarding the effect of CT and NT (Acharya and Sharma, 1994; Fuentes et al., 2003; Lawrence et al., 1994; Martínez et al., 2008; Merrill et al., 1996). In a two-year experiment on wheat, Hou et al. (2018) reported that CT and NT had a non-significant effect on R:S in the first year. However, shoots in the NT were significantly higher than CT in the second year, which significantly reduced R:S in the NT. In this regard, Muñoz-Romero et al. (2010a) argued that shoot growth of wheat was more sensitive to weather conditions under NT, particularly to rainfall, while the influence of rainfall on root growth is lower. Similarly, Bocianowski et al. (2018) reported that the interaction of tillage and year influences the harvest index. These findings indicate that the diverse responses of CT and NT on the R:S of a crop species are very dependent on the site, climate, year and cultivar (Jin et al., 2007; Nawaz et al., 2024).

Some experiments have shown that wheat/corn yield has been higher in the wet years under CT, but in dry years the wheat/corn yield was higher under NT (De Vita et al., 2007; Ordóñez Fernández et al., 2007; Muñoz-Romero et al., 2010b; Page et al., 2019; Pittelkow et al., 2015; Ramos et al., 2019; Su et al., 2021). Vizioli et al. (2021) and Pearson et al. (1991) also pointed out that root growth would be retarded under NT but eventually, root growth would be better under NT than CT because of long-term changes in soil structure and infiltration characteristics. Therefore, time after tillage treatment is a central player in the R:S studies of field crops as shoots respond more quickly to climatic variations than roots (Hamblin et al., 1990; Muñoz-Romero et al., 2010b; Page et al., 2019). It is also noteworthy that the relationship between root and shoot mass may not be linear for all ranges of values. For example, Muñoz-Romero et al. (2011) over a 3-year study reported that there is a quadratic relationship between root and shoot masses such that beyond a threshold value of root mass, the shoot mass of faba bean will decrease. This finding also supports the argument of Xu et al. (2020) and Hu et al. (2018) that a fixed allometric relationship of R:S, which is often used to estimate root mass based on the aboveground yield, may fail in reality and could underestimate or overestimate root biomass.

Muñoz-Romero et al. (2011) reported that although the root mass and shoot mass of faba bean were significantly different under NT and CT, the effect on the R:S was not significant, which was also confirmed by Hou et al. (2018) for wheat. The results of Muñoz-Romero et al. (2011), Hou et al. (2018) and other researchers (e.g. Page et al., 2019) indicated that under NT and CT, soil moisture content is a major driver that controls root and shoot growth. Higher soil water content in wet years could significantly increase root growth under NT than CT, while the shoot mass may not significantly differ (Hou et al., 2018; Muñoz-Romero et al., 2011). Vice versa, in dry years and low soil moisture content, the root mass will not significantly differ under NT and CT, but NT may increase shoot mass more than CT. In agreement with this finding, Unger and Fulton (1990) in long-term NT and CT experiments in the dryland area of Texas reported that NT outperformed CT in wheat and sorghum production. A greater soil water storage under NT than CT is widely accepted and its effect on shoot increase could be one reason for lower R:S under NT conditions (Mondal et al., 2020; Page et al., 2019; Power et al., 1986; Ramos et al., 2019; Unger, 1984; Unger and Fulton, 1990). However, López-Bellido et al. (2007b,a) reported that NT was as efficient as CT in soil water storage and productivity under Mediterranean conditions. Mangalassery et al. (2015) reviewed 60 published experiments with paired NT and CT and realized that nearly half of the experiments reported yield advantage under NT and the other half reported yield advantage under CT. Debates on this topic may still continue, which calls for further studies on regional mapping and recommendations on NT and CT suitability for soil types, crop types, climate and field management (Galdos et al., 2019; Hobson et al., 2022; Kuhn et al., 2016; Nawaz et al., 2024).

In addition to reasons such as soil properties, growth stage, site specifications, crop management, genetics, and nitrogen fertilizer (Anderson, 1988; Gao et al., 2016; McMichael and Quisenberry, 1993; Plaza-Bonilla et al., 2014), another reason could be the root sampling depth. This issue underlines the importance of soil sampling and analysing in deeper soil layers below the plough layer. Lal (2009) suggested root sampling down to 100 cm depths because of deep rooting depths (100 to >150 cm) of different agricultural crops (Luo et al., 2010; Meurer et al., 2018).

However, CT may affect the rooting depth (Kadžienė et al., 2011; Munkholm et al., 2008; Pearson et al., 1991) such that more roots could penetrate the deeper soil layers compared with the NT system. In contrast, Muñoz-Romero et al. (2010b) found that in deeper soil layers the tillage systems did not affect root mass, and Lampurlanés et al. (2001), Page et al. (2019), and Vizioli et al. (2021) reported that NT showed greater root than CT not only in the upper soil layer but also in the deeper soil layers. These inconsistencies in the literature, along with currently limited knowledge on the effect of different tillage systems on the main crops (e.g., wheat) (Aixia et al., 2022), add uncertainties in the analysis of R:S under CT and NT. Further R:S observation at more diverse genotype × environment × management (G × E × M) combinations for gaining more details on root and shoot coordination and their influence on crop yield and soil health are suggested.

Last, studying root systems under field conditions is challenging because of restricted access to large root systems, time-consuming sample processing, and results that are difficult to interpret (Hobson et al., 2022; Lynch and Brown, 2001; Muñoz-Romero et al., 2010a). Consequently, our understanding of root mass distribution in the soil profile remains limited (Ahmadi et al., 2020; Schenk, 2008; Schenk and Jackson, 2002). Hirte et al. (2017) noted that extraneous organic matter could cause significant overestimation of root mass recovery. Despite these challenges, since root growth is strongly influenced by soil bulk density, NT and CT can significantly affect root growth, distribution, and propagation. This suggests a trade-off where increased topsoil root mass, which boosts root-based organic matter, might lead to lower grain yield and shoot mass in some cases (Blanco-Canqui and Ruis, 2018; Zhao et al., 2023) because of limitation of root development in subsoil, hindering rainwater infiltration, reduced crop stress resistance, and subsequently insufficient nutrient supply in the later growth stage and yield loss (Yang et al., 2021).

4.4 Conclusions

Our analyses showed that shifting from CT to NT had only very few significant differences of R:S in CT versus NT. Despite limited data, this meta-analysis suggests the need for more specific field experiments to understand the effects of different tillage systems on the R:S of field crops under diverse environmental stresses such as drought, heat, salinity, and nutrients, which may interact with the NT and CT. Analysis showed that crop type and soil texture have significant and diverse influences on R:S under CT and NT. Rapeseed and barley had higher R:S in NT, while maize and wheat had higher R:S in CT. Comparing the soil textures, silty clay, sandy loam and clay loam had significantly the highest R:S, while sandy clay loam, clay and loam had lower R:S. Dicot crops had a higher R:S ratio in NT versus CT, though not significant. Moreover, no significant differences were found between deep (>30 cm) and shallow (<30 cm) root sampling depths, indicating that the most fraction of root mass could be sampled in the shallow depth sampling. Further factors that impact the R:S ratio, including but not limited to, root and shoot sampling procedure and timing after treatment differentiation (into CT and NT), soil water content, climate and precipitation patterns, could be some of the sources of uncertainties in the reported R:S. Ensemble crop modelling practice is useful to investigate the interactions of genotype × environment × management for gaining more details on root and shoot coordination and their influence on crop yield and soil health.

Chapter 5

The overlooked effects of environmental impacts on root:shoot ratio in experiments and soil-crop models

This chapter has been published as:
Seidel, S., Ahmadi, S., Weihermüller, L., Couëdel, A., Lopez, G., Behrend, D., Kamali, B., Gaiser, T., & Hernández-Ochoa, I. (2024). The overlooked effects of environmental impacts on root:Shoot ratio in experiments and soil-crop models. *Science of The Total Environment*, 955, 176738. `https://doi.org/10.1016/j.scitotenv.2024.176738`

Abstract

Process-based soil-crop models are becoming increasingly important to estimate the effects of agricultural management practices and climate change impacts on soil organic carbon (C). Although work has been done on the effects of crop type and climate on the root:shoot (biomass) ratio, there is a gap in research on the effects of specific environmental or management conditions such as drought, temperature, nutrient limitation, elevated CO_2 or tillage on the root:shoot ratio and thus, atmospheric C sequestration. In this study, we quantified the effects of these factors on the root:shoot biomass ratio by reviewing the current literature, presented common simulation approaches and performed model simulations using different examples. Finally, we identified different research gaps with respect to the root:shoot ratio with the aim of better estimating and predicting atmospheric C sequestration. A predominantly positive response of the root:shoot ratio was observed in case of elevated CO_2 (∼12%), low soil N levels (∼44%), and drought (∼14%). Soil tillage did not affect root:shoot ratio of the major field crops but increased it by ∼15% in case of wheat. There are only few field studies on air temperature increase and the results vary widely (mean −48%). The responses of tested models to the mentioned effects root:shoot ratio were slightly positive in case of CO_2 elevation (0 to 2%) and tillage (0 to 8%), slightly to clearly positive in the case of drought and N limitation depending on the model (1 to 40%), and very variable in case of the air temperature scenarios. Our study reveals large model uncertainty (especially on temperature effects), particularly for below ground processes that highlight knowledge gaps in simulating root:shoot ratio. We advocate for the need of more model-oriented specific experiments under abiotic stresses to help model improvement. Such research effort would enable more robust and reliable root:shoot ratio simulations.

5.1 Introduction

Climate-smart use of agricultural soils has a great potential to become a managed sink for atmospheric CO_2. To increase soil organic carbon (SOC) stocks through agricultural activities is considered a negative emissions technology (Merante et al., 2017; Lal, 2019) and has led to the 4 per mille initiative launched at the COP21 aiming to increase SOC stocks by 0.4% annually (Minasny et al., 2017). At the same time, climate change-driven SOC losses to the atmosphere might hinder such benefit (Riggers et al., 2021). In soils, root-derived C inputs (roots, exudates, secretes) in deep soil layers are a major stable source of SOC, due to limited microbial activity with increased soil depths (Chen et al., 2020c; Yu et al., 2022). Other sources of C input besides roots are fertilizers (e.g., farmyard manure, compost), and above ground crop residues (e.g., stubbles, dead leaves) (Ranaivoson et al., 2017), which are incorporated mainly into the top soil.

On average, plants allocate 76% of C stocks to shoots and only 24% to roots (Mathew et al., 2017). Only few studies have investigated the quantitative relationship between plant C and SOC (Mathew et al., 2017). According to Kuzyakov and Domanski (2000), cereals transfer 20–30% of total assimilated C to the soil. Half of this amount is subsequently found in the roots and about one third in the CO_2 extracted from the soil by root respiration and microbial utilisation of root organic matter (Kuzyakov and Domanski, 2000). Based on experimental data of the Swedish Ultuna long-term continuous soil organic matter experiment, Kätterer et al. (2011) reported that root-derived C contributes more to relatively stable soil C pools than the same amount of above-crop residue-derived C. In their meta-analysis, Mathew et al. (2017) compared data of 389 field trials to determine allocation of biomass and C in plants and SOCs under fields of different crop types considering long-term mean annual precipitation and mean annual temperature, geographical location and soil properties (clay content, bulk density and pH). Grasses and cereals had the highest potential for C sequestration. Furthermore, the authors stated that the highest C sequestration would be expected to occur in tropical climates. Beside crop type and climate, agricultural management can affect soil C input dynamics in agricultural soils (Stockmann et al., 2013).

The application of dynamic carbon models to report changes in SOC stocks is becoming increasingly important (Jacobs et al., 2020; Keel et al., 2017; Riggers et al., 2019, 2021). However, there is a large uncertainty in soil carbon modelling related to the method of calculating plant C input in agricultural systems (Keel et al., 2017). Most process-based multi-compartment SOC models such as ROTH-C, Yasso, Candy carbon balance, or the IPCC equation describe SOC decomposition by first-order kinetics and define different SOC qualities represented by interacting SOC pools (Farina et al., 2021). C-pool decomposition rates are modulated by external factors, such as soil temperature, soil moisture (sometimes aeration), or soil texture (mostly clay content). These SOC models use crop-specific coefficients to quantify soil C inputs for above- and below-ground plant residues including exudates and dead roots (Keel et al., 2017). Additionally, these models assume either a linear relationship between yield and C input, or use a yield-independent C input (Keel et al., 2017), which increases the uncertainty when calculating C inputs as the method selection can lead to different results. This approach also constrains the modelling to soil processes and excludes the simulation of shoot and root growth responses to changes in the environment.

Process-based one-dimensional field-scale soil-crop models are composed of different sub-modules for certain processes related to crop growth and soil-nutrient and water dynamics in response to atmospheric conditions and management practices. Biomass increment can be affected by water and nutrients (mainly nitrogen, N) availability in a given physical environment (van Ittersum et al., 2003). Drought stress effects on crop growth are often quantified by the ratio between actual and potential transpiration and often lead to an increased dry matter allocation to root biomass while reducing leaf biomass (van Ittersum et al., 2003). Current model intercomparisons have shown that root simulations, and how roots impact SOC formation via root biomass residues, largely diverge among models (Couëdel et al., 2024). Process-based crop models simulate several of the above-mentioned C inputs and related processes such as shoot and root biomass production of main and catch crops, fertilizer input (including organic fertilizers like manure with defined C contents), and plant residue return to the soil. Several process-based crop models simulate also SOC turnover including soil respiration and microbial activity and microbial biomass production. Currently, only very few crop models consider root exudates, such as AgroC (Klosterhalfen et al., 2017), as a source of C to the soil. Several crop models also simulate the effect of tillage practices on soil states (Maharjan et al., 2018). Therefore, crop models can potentially capture in-season stress effects on the root:shoot ratio (calculated by dividing the total root biomass by the shoot biomass) and yield, and long-term feedbacks (legacy effects in crop rotations, C sequestration) of environment and management practices on total biomass and soil C input.

However, the simulation of effects of extreme climate events such as heat, drought, and excess water on crop growth, which are expected to become more frequent in the future, are not always well considered in crop models (Kim et al., 2024; Webber et al., 2022), therefore, predicting agronomic management impacts (e.g., fertilization, crop rotation) on agroecosystem performance under future environments poses an additional challenge (Peng et al., 2020). Although the effects of crop type and climate on atmospheric carbon sequestration have been studied (Bolinder et al., 1997, 2007; Kuzyakov and Domanski, 2000; Mathew et al., 2017), there is a lack of knowledge about the effects of atmospheric CO_2 elevation, air temperature change, drought, N deficiency and conventional tillage on the root:shoot ratio, which is also reflected in the modelling approaches and simulation capabilities.

For given inputs, variability in soil-crop model simulations arises from variability in the model equations (structure) and the used parameter values (Wallach et al., 2024; Wang et al., 2024b). To our knowledge, dry matter partitioning as a main source of uncertainty in climate change impact assessment for agricultural crop yield has not been investigated before. Consequently, there is an urgent need to evaluate and improve the simulation of the root biomass-derived soil C input, and therefore, atmospheric C sequestration potential considering environmental conditions and (changing) agricultural management practices.

In this study, we focused on testing the sensitivity of model equations to the different inputs for fixed model parameters. We i) review how the root:shoot ratio and the root biomass-derived C input via root biomass of common arable crops are affected by atmospheric CO_2 elevation, air temperature change, drought, N deficiency, and conventional tillage; ii) report how process-based soil-crop models account for these factors in their equations, and iii) compare and evaluate the sensitivity of four process-based soil-crop models to simulate the impacts of these factors on root:shoot ratio and absolute root biomass input in the soil in a scenario analysis.

5.2 Materials and methods

5.2.1 Observed effects of abiotic factors and tillage on root: shoot ratio of crops

In total, we found and reviewed 12 articles on the effects of atmospheric CO2 elevation (3 of them were meta-analysis or reviews), 7 of air temperature variation, 7 of drought (3 reviews), 13 of N deficiency, and 29 articles of soil tillage effects (no-tillage vs. conventional or reduced tillage) on root:shoot ratio of common agricultural crops observed under field conditions (or semi-natural conditions) (sources see supplementary material - Table D.1). The major outcomes of these factors on root:shoot ratios are presented in the following sub-sections.

Elevated atmospheric CO_2 levels

Enhanced atmospheric CO_2 generally leads to increased biomass growth and root: shoot ratios due to improved water use efficiency, which indicate a proportional stimulation of below-ground biomass production, though the magnitude of the response can vary among crop species (Figure 5.1) (Vanuytrecht et al., 2012). A review by Rogers et al. (1995) showed substantial variation in root:shoot ratio response to enhanced CO_2 for various crops, with a mean positive response of 7% (12% for <580 ppm). In 59.5% of the cases, the root:shoot ratio increased, whereas in 37.5% of the cases it decreased, and in only 3% of the cases it remained unchanged. However, most experiments were conducted under controlled conditions. Results from a meta-analysis on agricultural crops showed that aboveground biomass and root:shoot ratio increased substantially, by 15% and 14%, respectively, for elevated CO_2 between 541 and 580 ppm, and further increased by 35% when CO_2 ranged between 581 and 620 ppm (Vanuytrecht et al., 2012). Another meta-analysis in a wide range of ecosystems reported a significant root:shoot ratio increase of 12% for agricultural crops (Nie et al., 2013).

With regards to wheat, we identified only four field FACE studies that provide data on root:shoot ratio. Kou et al. (2007) used two atmospheric CO_2 concentration levels (350 and 550 ppm) and high or low N fertilizer. The reported root:shoot ratio declined between 2% (low N) and 8% (high N) in all treatments. In contrast, Ma et al. (2007) reported about 20% (low N) and 25% (high N) higher wheat root:shoot ratio under elevated CO_2, with the strongest increase observed between jointing to heading stages. As for spring wheat, Wall et al. (2006) reported increases in

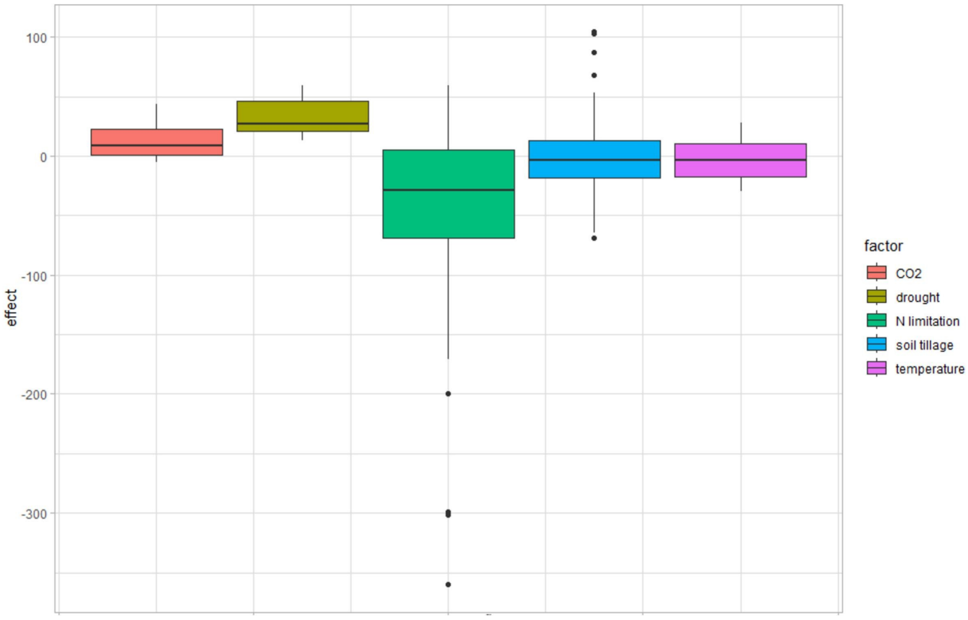

Figure 5.1: Effect of abiotic factors on observed root:shoot ratios of common agricultural crops under field and semi-natural controlled conditions in case of low data availability. The data show the percentage effect of ambient CO_2 elevation (number of data points $n = 15$), drought stress ($n = 7$), nitrogen (N) limitation ($n = 191$), increasing air temperature ($n = 10$) and conventional soil tillage (vs. no-tillage or conservative tillage, $n = 68$). The data source can be found in the supplementary material.

root:shoot ratio due to elevated CO_2 (ambient 370 ppm vs. ambient +180 ppm) by 10% and 3% under dry and wet conditions, respectively. But, during another growth period, elevated atmospheric CO_2 led to about 3% (dry conditions) and 7% lower (wet conditions) root:shoot ratio. In two open top chamber experiments with elevated CO_2, Rønn et al. (2003) reported a 2% decrease of root:shoot ratio, whereas Qiao et al. (2010) reported an increase of root:shoot by 22.8% and 9.1% under well-watered and drought conditions, respectively.

Considering these six FACE and open chamber wheat studies, a mean positive response of 5% on root:shoot ratio to elevated CO_2 was observed (Table 1, range: -5% to $+16\%$, $n = 9$). However, the root:shoot response of wheat, and other agricultural crops, to elevated CO_2 experiments is contradictory as evidenced by the wide range of results obtained from different studies. Additionally, CO_2 may interact with other factors such as water and nutrient supply, genotype, and plant age. For instance, legumes, root and tuber crops are expected to have a greater response to elevated CO_2 (Butterly et al., 2015; Rogers et al., 1995), with increased response under well-watered (23%) than under drought conditions (9%) (Qiao et al., 2010). In general, it was found that root:shoot ratio increased when increasing ambient CO_2 levels by a mean of 12–14% (Table 5.1).

Table 5.1: Effect of factors on observed (obs) root:shoot ratio (mean, minimum, and maximum differences) of common agricultural crops and of winter wheat observed under field conditions and semi-natural controlled conditions in case of low data availability. Simulated values are ranges of the applied models where each value represents the mean of the daily difference in % from end of tillering to end of flowering of winter wheat of the scenarios with the highest difference.

Factor	**Obs root:shoot of common crops**	**Obs root:shoot of winter wheat**	**Simulated in this study**
Elevated CO_2[1]	+12%, +14%, +12% (−11% to +47%)	+5% (−5% to +16%)[2]	0 to +2%
Drought occurrence	13.5% (+13% to +59%)[3]	+21% to +27%[4]	+1 to +40%
Nitrogen deficiency	+44% (−22% to +121%)[5]	+64% (+40% to 84%)[5]	+1 to +43%
Air temperature increase[5]	−20% to +26%[6]	−20% to −30%[6]	−30 to −86%
Soil tillage	0.5% (−104% to 69%)[7]	2.4% (−25% to 45%)[7]	0 to +8%

[1] Considering Rogers et al. (1995) and Vanuytrecht et al. (2012) with CO_2 increase <580 ppm with 12% and Nie et al. (2013).

[2] Considering only the six FACE and open top chamber studies.

[3] Based on the review of Zhou et al. (2018).

[4] Based on Fang et al. (2017).

[5] Based on Lopez et al. (2023).

[6] Air temperature increase compared to normal conditions/control. Based on Füllner et al. (2012) and Rehman et al. (2019).

[7] On average, CT (conservative and conventional tillage) increased root:shoot ratio in wheat by 14.8% compared to NT (no-tillage) based on 8 studies with $n = 16$ data pairs. Considering only winter wheat, the increased root:shoot ratio is only 2.4% (4 studies, 9 pairs).

Water supply and drought

Drought is one of the main abiotic stress factors in agriculture, which negatively affect crop growth and development, and therefore, crop productivity (Fahad et al., 2017; Farooqi et al., 2020). Changes in root architecture and distribution are important mechanisms to cope with drought stress in crops (Dietz et al., 2021; Matsui and Singh, 2003; Siddiqui et al., 2024), as well as changes in root:shoot ratio (Seleiman et al., 2021). In a synthesis of global field trials synthesizing data from 128 published studies, Zhou et al. (2018) showed that drought significantly decreased root length and root length density by 38% and 11%, respectively, but increased root diameter by 3.5%.

In general, root:shoot ratio tends to increase under drought conditions, but the magnitude of increase depends on the crop as well as on timing and magnitude of the stress. Kou et al. (2022) reported that under drought stress conditions, crops with fibrous root systems resulted in a 22% increase in root:shoot ratio, while in crops with tap root systems, the root:shoot ratio increased by 43%. Zhou et al. (2018) reported that drought stress tends to increase the root:shoot ratio by 13.5% (Table 5.1), with a wide range of variation depending on the crop and magnitude of drought stress. Additionally, root:shoot ratios responded negatively to drought at <25% intensity (moderate drought stress), but increased at 25–50% and >50% intensity (severe drought stress). Root:shoot ratio increased in wheat when drought stress was applied during the vegetative stage, which resulted in an increased crop growth rate due to the higher root water uptake and gas exchange (Bacher et al., 2022). Fang et al. (2017) reported different responses to moderate drought stress (rainfed vs. irrigated) in an old and a modern winter wheat cultivar grown under field conditions, where the root:shoot ratio increased in the old cultivar by 27% and increased in the modern cultivar by 4%. For legumes, a similar response of increasing root:shoot ratio under drought stress has been reported although some crop legume species, like cowpea, are more tolerant to drought stress (Du et al., 2020; Matsui and Singh, 2003; Pang et al., 2011). Root length density, root depth, and root dry matter can potentially be used for selection of drought tolerance cultivars (Matsui and Singh, 2003). However, selection for increased root:shoot ratio can be challenging. A study conducted with 99 wheat genotypes showed a negative correlation between root:shoot ratio and grain yield, high environmental variance, and low heritability as limitations for breeding cultivars to have more root biomass and maintain grain yield under drought conditions (Mathew et al., 2018).

Nitrogen supply and soil nitrogen limitation

Plant root characteristics play a crucial role in acquisition of resources and plant performance, especially when the availability of nutrients in the soil is low. Several field studies on the effect of N deficiency report increased root:shoot ratio (Welbank and Williams, 1968; Myers, 1980; Anderson, 1988; Eghball and Maranville, 1993; Sharifi et al., 2005; Wang et al., 2005; Farrior et al., 2013; Xue et al., 2014; Hadir et al., 2020). In a meta-analysis of 50 field studies considering nitrogen (N), Lopez et al. (2023) found that the root:shoot ratio was often enhanced (mean of 44%, based on 13 studies) under N-poor conditions. Two studies conducted by Anderson

(1988) and Eghball and Maranville (1993) reported an increase in the root:shoot ratio of maize under nitrogen-deficient conditions, particularly in low N conditions. Anderson (1988) observed a significantly higher root:shoot ratio in unfertilized trials compared to the high fertilization (application of 180 kg N per ha) across three years of evaluation. In winter wheat, Xue et al. (2014) also observed an increase in the root:shoot ratio with decreasing N supply. The data are similar to those provided by Wang et al. (2014), who found that no fertilization treatments significantly increased the root:shoot ratio in winter wheat. However, N applications were particularly beneficial for the shoots, leading to a decrease in the root:shoot ratio when N was applied (Welbank and Williams, 1968).

While most studies have reported an increase in the root:shoot ratio under N deficiency, few studies have found variable effects on the ratio depending on other factors studied. Feng et al. (2016) reported that maize root:shoot ratio at silking was higher in the no fertilization treatment, except in the loamy clay soil in one out of the three years of the study. In sugarcane, N deficiency led to a decrease in the root:shoot ratio at the beginning of the production cycle at one out of two experimental sites, with similar ratios observed between treatments in later growth stages (Otto et al., 2014). In general, Lopez et al. (2023) reported that root:shoot ratio increased with decreasing N level by a mean of 44% and 64% for wheat (Table 5.1).

Air temperature

Air temperature is an important factor for phenological development and above and below plant growth (Gregory, 2007). Optimal temperature ranges, and thus, the effect of temperature on the root:shoot ratio, seem to differ strongly between crop species (Koevoets et al., 2016). For wheat, reported optimal air temperatures for root growth range around 16.3 (±3.7)°C, while optimal air temperatures for shoot growth range around 20.3 (±0.3)°C (Porter and Gawith, 1999). Under non-optimal root zone temperatures, root:shoot ratios increased compared with optimum temperature ranges (Koevoets et al., 2016). In a pot study with barley, Füllner et al. (2012) found a 21% (from 0.39 to 0.31) mean decrease in root:shoot ratio when changing the root temperature from 10°C to 20°C. In another pot experiment where air temperatures were increased from 25/20°C (day/night) to 36/28°C, Rehman et al. (2019) observed a root:shoot ratio decrease of 20% and 30% in two wheat cultivars. These changes in root:shoot ratios might, however, not be directly related to temperature but adaptations to restrictions in water and nutrient uptake (Wilson, 1988; Equiza et al., 2001; Fonseca de Lima et al., 2021).

While the previously listed studies can give us a good understanding of physiological responses of roots and of the root:shoot ratio to changes in temperature, these experiments are also limited in transferability as they have been conducted under controlled conditions in pot experiments. One of the main differences between field trials and most pot experiments is the temperature gradient in natural soils, where temperature is not uniform but changes with depth. In a pot study with and without temperature gradients, Füllner et al. (2012) observed that barley roots exposed to a vertical gradient in soil temperature of 20–10°C had a 161% higher root:shoot ratio than plants grown under uniform soil temperature of 20°C. Additionally, observations from most pot experiments are focusing on early developmental stages. Although widely accepted methodologies to alter soil and atmospheric temperatures under field conditions exist (Patil et al., 2013), field experimentation on root growth remains rare. In a study where two maize varieties were grown in buried pots in three environments with mean air temperatures of 14.6, 16.9, and 18°C respectively, Richner et al. (1996) observed highest root:shoot ratios under mean air temperatures of 14.6°C at the four-leaf stage. Ordóñez et al. (2020) reported a positive correlation between temperature and root:shoot ratios in a study with maize and soybean at 10 different sites in the U.S. state of Iowa. Hou et al. (2018) applied infrared heaters 3 m aboveground for two years and an interaction between temperature and tillage on root biomass distribution of winter wheat was reported, with significantly higher root biomass in the upper 0–10 cm under no tillage and warming and significantly higher root biomass between 10 and 30 cm under tillage and warming, but no variation was observed in the root:shoot ratios (Hou et al., 2018).

Soil tillage

Conventional tillage (CT) system with heavy machinery can result in subsoil compaction that limits water infiltration and restricts crop root growth, and therefore, affects biomass yield (Zhang et al., 2024a; Horn, 2004; Horn and Smucker, 2005). The response of root:shoot ratio to tillage systems is complex and strongly depends on soil texture (Zhao et al., 2023; Schneider et al., 2017), soil bulk density (Oussible et al., 1992; Qin et al., 2004; Alvarez and Steinbach, 2009), weather and climate conditions (Álvaro Fuentes et al., 2007; Muñoz-Romero et al., 2010b), soil moisture and temperature (Liu et al., 2015; Guan et al., 2014; Hou et al., 2018), soil nutrient status (Oussible et al., 1992; Haugen-Kozyra et al., 1993; Schneider et al., 2017; Muñoz-Romero et al., 2010b), and crop type (Álvaro Fuentes et al., 2007; Andersen et al., 2013). Therefore, assigning a single root:shoot ratio for specific crops without considering the tillage effect could result in biased estimation of root-induced carbon to the soil, especially for modelling soil organic carbon storage and changes.

Generally, conservative and conventional tillage (CT) tends to increase root:shoot ratios for cereals by about 4% (based on 19 studies with 45 root:shoot ratio data pairs, see supplement). In a 3-year study, Muñoz-Romero et al. (2010b) studied the effects of root growth under CT and no tillage (NT) for spring wheat under rainfed conditions and the results showed higher root biomass in the topsoil layer under CT, but no differences were observed in deeper soil layers. Additionally, the root:shoot ratio was lower in the NT vs. CT (0.13 vs. 0.18) due to increased shoot biomass. Rotary tillage before seeding increased the axile root:shoot ratio by 16% in maize as reported by Bian et al. (2016). Despite that in most cases CT increases root:shoot ratios of cereals including maize, studies have also found the opposite or no response to tillage (based on 21 studies with 46 root:shoot ratio data pairs). Hou et al. (2018) found no significant differences in one of two years in irrigated winter wheat, whereas Wilhelm (1998) stated that NT increased the root:shoot ratio of winter wheat by 24% compared to CT. Other studies reported no difference in root:shoot ratio of winter wheat under NT and CT under temperate climate (Ellis and Barnes, 1980; Qin et al., 2004).

On average, soil tillage (conservation and conservative tillage) decreased root:shoot ratio only by 0.5% as compared to no-tillage among several field crops under diverse environmental conditions (based on 29 studies with 68 root:shoot ratio data pairs). In case of legumes, tillage decreased root:shoot ratio by 13% as compared to no-tillage (House et al., 1984; Muñoz-Romero et al., 2012; Das et al., 2021; Adamič and Leskovšek, 2021). Specifically for wheat, soil tillage increased root:shoot ratio by about 15% as compared to no-tillage (9 studies with 18 root:shoot ratio data pairs). Considering only winter wheat, tillage increased root:shoot ratio by about 2.4% as compared to no-tillage (Table 5.1).

5.2.2 Implementation of the effect of abiotic environmental stresses and tillage on root:shoot ratio in simulation models

Experimental data used for model calibration

The experimental data were taken from a field trial conducted at the agricultural research station Campus Klein-Altendorf of the University of Bonn, situated in western Germany at 50°37′ N, 6°59′ E, and 176 m altitude. Winter wheat (*Triticum aestivum*) cultivar cv. Milaneco was sown on August 29^{th}, 2020 and harvested on August 8^{th}, 2021. The shoot data used for the current study included leaf area index (LAI) collected four times, shoot biomass measured five times, and straw and grain yield at harvest. Root sampling was carried out on May 19^{th}, 2021 using a root auger with an inner diameter of 9 cm and a length of 1 m; the root biomass and root length density were determined. Details on the experimental site, the trial, and the data collection and post-processing can be found in the supplementary material.

Selected crop growth models

For the modelling exercise, the process-based soil-crop models STICS, SIMPLACE, AgroC, and MONICA were selected. They are process-based agroecosystem models (or soil-crop models) that represent main processes related to crop development and growth and the interactions with the environment. Typically, biomass production is a function of radiation and temperature. The growth may be further modulated by radiation use efficiency, temperature and CO_2 response curves, as well as water and nutrient stresses (Jamieson et al., 2008). Common main processes implemented in these 1D field-scale crop models are outlined in the supplementary material.

Model setup and calibration (baseline scenario)

Weather data, soil characteristics and initial volumetric soil water content from the experiment explained above were provided as input. The models were calibrated separately by adjusting the phenology parameters to match the observed dates for emergence, flowering, and physiological maturity. As for crop growth, intermediate and final above-ground biomass, root biomass, LAI and final grain yield were used for the model calibration. The calibrated models were then applied for the scenario runs.

Model scenarios

Five scenarios with respect to ambient CO_2 enhancement, changes in air temperature and precipitation, N availability, and tillage were generated. Only one input (e.g., air temperature) per scenario was changed and the others (e.g., CO_2 concentration) were kept constant. Model parameters (such as crop parameters) were held constant throughout the scenario runs in each of the models, allowing only the effect of the varying input to be studied. One exception was the temperature scenarios: the phenology parameters were adjusted so that the flowering and harvest dates were always the same in all scenarios, to allow better analysis and interpretation of the root:shoot ratios.

The baseline was considered as the simulation with the original input data (see Section 5.2.2). For the atmospheric CO_2 concentration, 11 scenarios ranging from 424 to 570 ppm, with a 3% (13-16 ppm) increase by scenario were created. For the precipitation scenarios (drought and excess water), the mean daily precipitation was reduced and increased by 10, 20, 30, 40, and 50% from the baseline. In the case of the temperature scenario, the mean daily temperatures were increased and reduced from the baseline by 1, 2, 3, 4, and 5 °C, respectively. For the N availability scenario, the initial soil N (0–90 cm) and the applied mineral fertilizer were set to (initial soil N/applied N fertilizer) 0/0, 25/0, 50/0, 0/50, 25/50, 50/50, 0/100, 25/100, 50/100, 150/140 (baseline), and 200/200 $\mathrm{kg\,N\,ha^{-1}}$. Finally, for the tillage scenario, the topsoil (0–27 cm) bulk density ranged between 1.14 and 2.06 $\mathrm{g\,cm^{-3}}$, with continuous increments of 6% by scenario. For the tillage scenario, the respective topsoil hydraulic properties were generated using the Hypres pedotransfer functions (Wösten et al., 1999).

To allow for a better comparison with observations, we calculated the mean of the daily difference between the scenarios with the highest difference per model in a period where root observations in the field often take place, namely from end of tillering to end of flowering, which relates to May 5th to June 24th, 2021.

5.3 Results and discussion

5.3.1 Scenario results

Simulated root:shoot ratios in the baseline scenario

In general, the shape of the simulated root:shoot ratio curves as well as the maximum absolute root:shoot ratio values varied widely among the models (Figure 5.2). For the baseline from March 1st to harvest, the maximum absolute root:shoot ratio values were: AgroC = 0.3, STICS = 0.4, MONICA = 1.1, and SIMPLACE = 1.4. Strong differences in simulated root:shoot ratio over the entire growing season were observed especially in early growing stages before March 1st. The mean winter wheat root:shoot ratio provided by the meta-analysis of Mathew et al. (2017) was 0.30. Bolinder et al. (1997) reported winter wheat root:shoot ratios of 0.13–0.2 measured at or close to maturity in field studies, and Hirte et al. (2021) reported a root:shoot ratio of 0.09 at flowering of winter wheat (conventional farming). Thus, the simulated root:shoot ratios in the later growth stages were in the range of reported values.

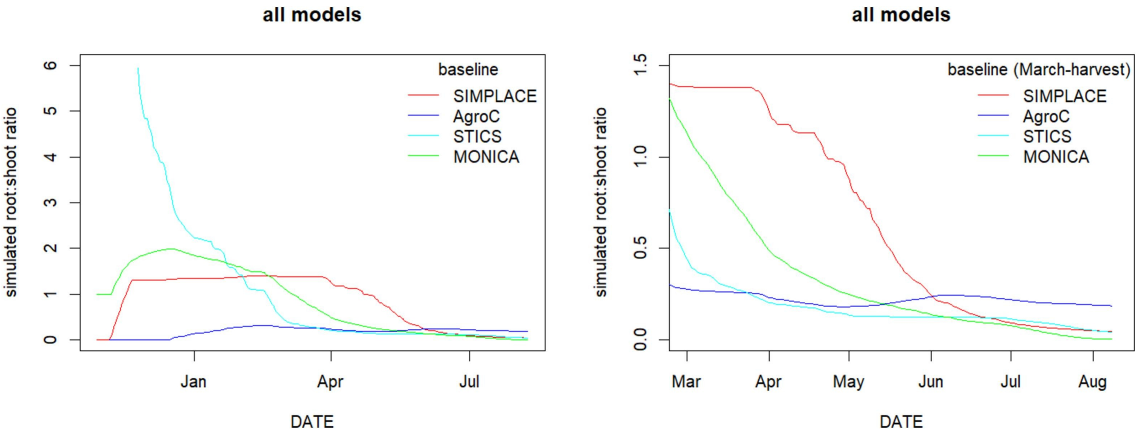

Figure 5.2: Simulated daily root:shoot ratios for STICS, SIMPLACE, AgroC, and MONICA models for the baseline scenario from emergence to harvest in August (left) and from March 1st until harvest in August 2021 (right).

Atmospheric CO_2 levels

The simulated root:shoot ratios for changes in atmospheric CO_2 levels only differed marginally from those simulated under the baseline scenario for all models (Figure 5.3, and Figures D.1, D.2, D.3 and D.4 in the supplement). The mean difference (mean of the highest difference of all eleven scenarios per day) was 1.5% for MONICA, 3% for STICS, and 1% for SIMPLACE, with peaks at harvest of 3% for MONICA, STICS, and SIMPLACE. AgroC did not consider feedbacks of changing atmospheric CO_2 concentrations on crop growth in the version used in this study. From end of tillering to end of flowering, the root:shoot ratio was affected by 0% for STICS, 1% for SIMPLACE, and 2% for MONICA, pointing again to the fact that changes in CO_2 concentration will not impact the root:shoot ratio substantially in the models. An absolute shoot biomass (Figures D.11, D.12, andD.13) and root biomass (Figures D.7, D.8, and D.9) increment with increasing ambient CO_2 enhancement was simulated by STICS, SIMPLACE, and MONICA.

Water supply and drought

The root:shoot ratios simulated with SIMPLACE were very sensitive to changes in precipitation (Figure 5.3). The maximum difference among scenarios was 53% for the root:shoot ratio simulated in mid-May, as the root biomass was low in the scenarios which received very little rainfall but shoot biomass was similar within all

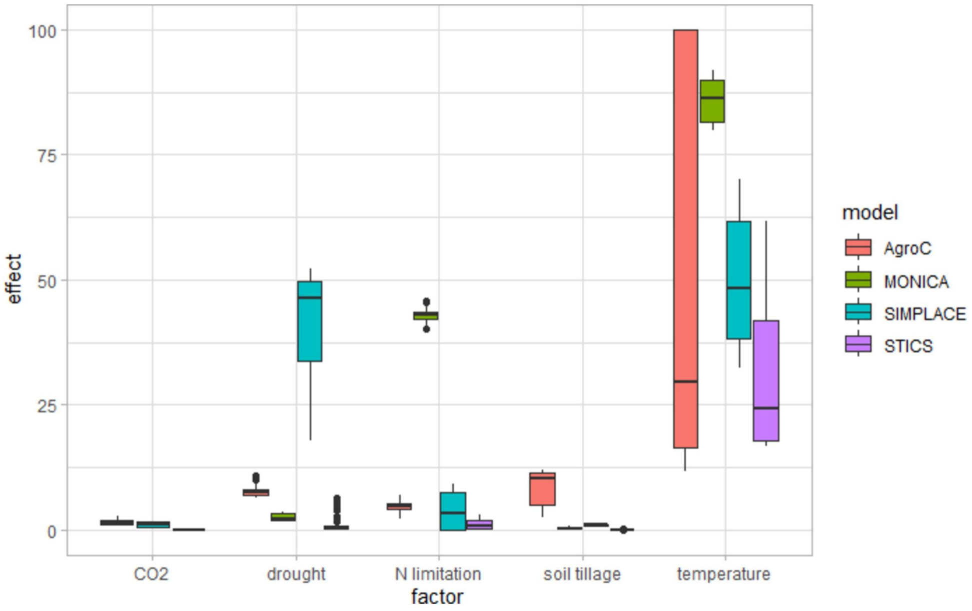

Figure 5.3: Maximum simulated winter wheat root:shoot difference in % for each factor across the scenarios (e.g., the 10 atmospheric CO_2 elevation scenarios) for four soil-crop models. Each boxplot represents the maximum difference among the 10 scenarios from 5th May to 24th June 2022 (daily values) per model.

scenarios. At harvest, the shoot and root biomass were proportionally reduced in the scenarios with lower precipitation. Also, the STICS and AgroC model results showed a moderate to strong sensitivity of root:shoot ratios to drought stress. The mean difference of root:shoot ratios in the scenarios with changing precipitation was 12% (season mean), with a maximum difference among scenarios at harvest of about 65% for the STICS model. The mean difference of root:shoot ratios in the rainfall scenarios in AgroC was slightly lower at 11%, and the maximum difference among scenarios was ∼50% simulated after emergence, which decreased over time and increased again around DVS 1.5 up to 15% at harvest (scenario 3 vs. scenario 8). MONICA showed the lowest response with a 2% mean difference of the root:shoot ratios for the precipitation scenarios. The maximum difference among scenarios was about 7% simulated for end of November, with another peak of differences of 5% at harvest by MONICA.

From end of tillering to end of flowering, the root:shoot ratio stayed relatively unaffected for STICS (1%) and MONICA (1%), whereas AgroC simulations showed a slightly larger difference (8%), and the largest was simulated by SIMPLACE with 40%. A decline of the absolute root (Figures D.6, D.7, D.8 and D.9) and shoot biomass (Figures D.10, D.11, D.12 and D.13) with increasing dry conditions was simulated by all models. The only exception was MONICA, which showed no decline of root biomass with increasing drought.

Nitrogen supply and soil nitrogen limitation

The MONICA model reacted most to N limitation (Figure 5.3). The simulated root:shoot ratios differed by a maximum of ∼50% at harvest with a daily mean difference of 20% for the MONICA modelling results. The root:shoot ratios in the N scenarios simulated by STICS differed by a maximum of ∼30% at harvest with a daily mean difference of only 4%. Intermediate differences were calculated by the SIMPLACE model, with maximum root:shoot differences of 20% at harvest (scenario 1 vs. scenario 11). The root:shoot ratios simulated by SIMPLACE only started to differ after mid-May at DVS 0.5, as the shoot growth started to differ among the N scenarios (more shoot growth in scenarios with higher N availability), whereas the root biomass was similar for all scenarios. As for AgroC, the simulated root:shoot ratios differed by a maximum of only 11% at harvest (scenario 1 vs. scenario 11).

From end of tillering to end of flowering, the root:shoot ratio was affected by 43% for MONICA, which was much larger than those simulated for the other models: 1% for STICS, 4% for SIMPLACE, and 5% for AgroC. A decrease in absolute root biomass with increasing N availability was simulated by all models (Figures D.6, D.7, D.8 and D.9). The only exception was SIMPLACE, which showed no decrease in root biomass with increasing N limitation.

Air temperature

The simulated root:shoot ratio was most sensitive to air temperature decrease and increase compared to all other environmental impacts analyzed (Figure 5.3, Figures D.1, D.2, D.3 and D.4 in the Supplementary Information). The impact of variations in air temperature on the root:shoot ratio already began at or soon after emergence. Both absolute root and shoot biomass were affected. A linear decrease of root:shoot ratio from scenarios 1–5 (lower temperature than baseline) and an increase from scenarios 7–11 (higher temperature than baseline) were observed for AgroC and SIMPLACE. The difference in root:shoot ratio at harvest between scenario 6 (baseline) and the scenario with the highest temperature increase (scenario 11) was 50% for SIMPLACE and 13% for AgroC. The decline in root:shoot ratio from end of tillering to end of flowering between scenario 6 (baseline) and scenario 11 was 50% for both SIMPLACE and AgroC.

By contrast, in the case of STICS and MONICA, increasing temperature (scenarios 1 to 11) led to a linear decline of root:shoot ratio, resulting in multiple times lower values in the high-temperature scenarios at harvest, and a mean root:shoot difference from end of tillering to end of flowering of 86% for MONICA and 30% for STICS. A decrease in absolute root biomass in the later growth stages with increasing air temperature was simulated by all models. The only exception was SIMPLACE, which showed an increase in root biomass. An increase in absolute shoot biomass with increasing air temperature was simulated by all models except AgroC.

Soil tillage

The simulated root:shoot ratios for the tillage scenarios were only slightly sensitive in the case of AgroC, SIMPLACE, STICS, and MONICA model outputs (Figure 5.3). Tillage affected early root:shoot ratios in the AgroC and SIMPLACE outputs, and late root:shoot ratios in the STICS and MONICA models. The mean difference of root:shoot ratios in the tillage scenarios was 12% (daily means comparing the scenarios with maximum differences of root:shoot ratios). The maximum difference of root:shoot ratio in the tillage scenarios was 6% (scenario means of root:shoot ratios), with a maximum span of 25% (scenario 1 to 5 vs. scenario 11) shortly after emergence for the SIMPLACE simulation results. Much lower differences in the mean root:shoot ratios for the tillage scenarios, with 1% and a maximum span of 2% at harvest, were reported for the MONICA model. Similarly, the STICS model showed a mean difference of the root:shoot ratio of 2% (daily means comparing the scenarios with maximum differences of root:shoot ratios), but a much wider span with a maximum value of 22% at harvest (scenario 1 vs. scenario 11). From end of tillering to end of flowering, the root:shoot ratio was affected by 0.5% for MONICA, 0% for STICS, 1% for SIMPLACE, and slightly larger with 8% for AgroC.

As AgroC solves the Richards equation for soil water dynamic calculations, it may be more sensitive to changes in the soil hydraulic characteristics induced by bulk density changes compared to the bucket-based models.

5.3.2 Simulated maximum absolute root biomass responses to abiotic stresses and tillage

The simulated maximum absolute root dry matter biomass in the season (potential root-C input into soil excluding exudates and secretes) plays an important role in simulating SOC dynamics and carbon sequestration. As the root:shoot ratio is affected by both root and shoot biomass, we explored whether the effects were rather on simulated absolute root or shoot biomass.

On average, the total C input in the soil by winter wheat roots (6 t ha^{-1} grain yield) is about 1200 kg ha^{-1} within one growing season (Kuzyakov and Domanski, 2000). The simulated maximum root dry matter biomasses in the baseline scenarios were 1.3 (MONICA), 1.7 (STICS), 1.9 (SIMPLACE), and 3.9 t ha^{-1} (AgroC) (Figure D.5). Assuming a 40% C content in the dry matter of the roots (Kuzyakov and Domanski, 2000), this corresponds to approximately 520 kg C ha^{-1} (MONICA), 680 kg C ha^{-1} (STICS), 750 kg C ha^{-1} (SIMPLACE), and 1560 kg C ha^{-1} (AgroC). Of the four models, only AgroC simulates root exudates. The total C amounts translocated into the soil by winter wheat (6 t ha^{-1} grain yield), including exudates, rhizodeposits, and root and rhizomicrobial respiration, is about 1500 kg ha^{-1} (Kuzyakov and Domanski, 2000). In AgroC, the total amount of root exudates transferred to the soil is a function of glucose assimilated and is defined as 5.3% of the total glucose assimilated. Thus, an additional 525 kg ha^{-1} of C (baseline) is translocated to the soil via the exudates during the winter wheat season in AgroC.

In the case of air temperature, simulated absolute root biomass was highly affected (Figures S5–S10). Although the simulated shoot dynamics and absolute values, including yield, were similar among the models (baseline), the simulated absolute root biomass values over time differed widely among the models (Figure S5). In general, dry conditions decreased absolute root biomass in SIMPLACE, STICS, and AgroC, but not in MONICA. On the other hand, low N conditions decreased absolute root biomass simulated by STICS, MONICA, and AgroC, but not in SIMPLACE. The simulated absolute maximum root dry matter biomass was strongly negatively affected by drought and N limitation in most models. Drought decreased the absolute maximum root biomass by up to 70% in AgroC, 60% in SIMPLACE and STICS, and 1% in MONICA considering all drought scenarios (scenarios with reduced precipitation). Also, the N deficiency affected maximum root biomass negatively (decline of up to 55% in STICS, 53% in MONICA, 50% in AgroC, and 2% in SIMPLACE).

Soil tillage (here reflected by decreasing soil bulk density and respective changes in the soil hydraulic characteristics) fostered a slight increase of absolute maximum root biomass of up to 11% for AgroC, 9% for STICS, and 2% for SIMPLACE, but no change was detectable for the MONICA simulation results. Elevated atmospheric CO_2 increased simulated absolute maximum root biomass by up to 13% for SIMPLACE, 10% for MONICA, and 7% for STICS considering all scenarios. An increase of air temperature led to an increase of absolute maximum root biomass of up to about 300% for SIMPLACE, 600% for AgroC, 47% for STICS, and 35% for MONICA.

5.3.3 Comparison of observed and simulated responses to changing environments

According to our literature research, Table 5.1 summarizes the observed and simulated effects of abiotic factors in common crops and, in particular, for winter wheat. Results show that, in general, root:shoot ratio increases under elevated CO_2, drought, and N deficiency, while it tends to decrease with temperature above the optimum. Tillage resulted in a minimum effect on root:shoot biomass ratio.

According to the model scenario results, the effects of abiotic factors and tillage on simulated winter wheat root:shoot ratios (mean values from end of tillering to end of flowering) were as follows: The root:shoot ratio (i) increased slightly by up to 2% in case of elevated atmospheric CO_2 concentrations, (ii) increased slightly to moderately (1 to up to about 40%) in case of increasing drought and N limitation, (iii) decreased moderately to strongly in case of increased air temperatures, and (iv) increased slightly to moderately (mean change of 0 to 8%) in case of tillage. Thus, the wheat root:shoot biomass responses seem to be adequately simulated in case of atmospheric CO_2 increase and tillage, moderately in case of drought (depending on the model being used), and rather underestimated in case of N limitation, with also a high variation in simulated results among the models. For air temperature increase (above the average), the models reproduced the negative effects on root:shoot ratio, but the observations and the model simulations varied widely (Table 5.1 and Figure 5.3). Observations, though scarce, suggest a decrease of root:shoot ratio of 20 to 30% in wheat under warmer conditions.

Mathew et al. (2017) revealed a significant negative correlation of root:shoot ratios with mean annual precipitation and SOC, but a significant positive correlation with soil pH and mean annual temperature. We report a root:shoot ratio increase by a mean of 14% under drought conditions versus well-watered conditions, in line with Mathew et al. (2017) who suggest an increase of root:shoot ratio with decreasing mean annual precipitation. Similar to the results in our study, the root:shoot ratios were often strongly increased under N deficiency (Lopez et al., 2023). An increase in the root:shoot ratio due to stress (drought, N deficiency) may be a result of increased C allocation to the roots leading to an increase in root biomass. According to the 'functional equilibrium' theory, plants increase the allocation of resources to maintain the development of the organ under stress as a way of counteracting the effects of stress (Poorter and Nagel, 2000).

According to our literature research, the effects of increasing air temperature on root:shoot ratio vary widely and also in different directions (-20% to $+26\%$). Mathew et al. (2017) reported a significant positive correlation of root:shoot ratio with mean annual temperature. We need to keep in mind that trials were conducted in temperate and (sub)tropical climates, whereas in our study we considered studies with treatment pairs of low and high temperature. In our review, root:shoot ratio decreased only by 0.5% in case of conventional tillage vs. no-tillage, which is in line with Mathew et al. (2017) who reported a non-significant positive correlation of root:shoot ratio with soil bulk density.

5.3.4 Model evaluation

RUE correction factors for atmospheric CO_2 enhancement are implemented in SIMPLACE, STICS, and MONICA. This approach (or the applied model parameters) seems to underestimate the effect of atmospheric CO_2 enhancement on root:shoot ratio, especially the absolute increase in root biomass. AgroC does not consider elevated CO_2 effects on crop growth.

The simulated effects of drought stress on the root:shoot ratio were moderate and in a similar range to the observations. SIMPLACE explicitly considers the effect of drought stress on root:shoot ratio via a root factor that leads to a higher C allocation to the roots (Figure 5.3). This leads to strong effects on root:shoot ratio of up to 40% in the driest scenario. In AgroC, the root:shoot ratio is predefined and drought effects are not explicitly considered. The simulation results indicate no or only a very minor effect of drought stress on root:shoot ratio, but a clear effect on absolute root biomass. In MONICA, a drought stress factor, which varies by developmental stages and organs, influences assimilation, but drought stress effects are not explicitly considered. Thus, despite that the models MONICA and SIMPLACE are able to capture directly the drought effects on C allocation into the roots, the simulated responses widely vary.

The observed N limitation effects on root:shoot ratio were moderately to high (mean of 44% for all crops and 64% for wheat), whereas the simulated ones ranged from 1 to 43%. In SIMPLACE, the fraction of biomass transferred to the leaves is reduced by a factor in case of low N conditions. However, this led to a minor effect on root:shoot ratio (4% from end of tillering to end of flowering). For AgroC and STICS, no explicit approach is implemented and the assumed N deficiency affected root:shoot ratio by 5% and 1%, respectively. MONICA was the only model where N deficiency led to a clear effect on root:shoot ratio. MONICA uses a crop reduction factor for nitrogen stress that also reduces root growth when tissue N concentration falls below a defined threshold (Eq. S13). This apparently favorable approach leads to a proportionally stronger decline in shoot than in root biomass (Figures D.7 and D.11).

Simulated soil tillage barely affected root:shoot ratio, which was similar to the observations for winter wheat (∼2.4% increase) (Table 5.1). Decreasing soil bulk density (soil tillage scenarios, soil hydraulic parameters were also affected) did not or only slightly increase simulated root:shoot ratios for STICS, AgroC, and MONICA. With regard to SIMPLACE, which accounts for soil strength, the root:shoot ratio was mostly affected in the early development stages before shoot stem elongation. We therefore assume that, for winter wheat, the model equations applied can reproduce the effects of soil tillage well.

Increasing and decreasing air temperatures (from the average baseline value) decreased observed root:shoot ratio by 20–30%. Air temperature affects the simulation of crop growth in various ways, e.g., via the temperature-driven crop development, or RUE correction factors for temperature to account for heat stress, but also via effects on soil N mineralisation. Air temperature decrease from 0°C to −5°C led to a stepwise decrease of root:shoot ratio in all models. While the daily increase from 1 to 5°C led to an increase of root:shoot ratio for AgroC and SIMPLACE with maximum differences of root:shoot ratios at harvest of 50% (SIMPLACE) and 13% (AgroC). In the case of STICS and MONICA, increasing temperature led to a linear decline of root:shoot ratio when comparing all eleven scenarios (FiguresD.3 and D.4).

5.3.5 Suggestions for model improvement

The high variability and uncertainty of the modelling results (Figure 5.3), especially for temperature, drought, and N limitation scenarios, indicate a clear need to fill research gaps with regards to the impacts of abiotic stress, particularly in below-ground dynamics for root:shoot ratio and absolute root biomass growth, and consequently, the need for model improvement. Our results are in line with previous model intercomparison showing large differences among models when simulating root:shoot ratio and crop-to-soil feedback (Couëdel et al., 2024). We call for more systematic field experiments, particularly on the effects of single abiotic stress and their interactions, considering the effects on shoot and root growth, as well as their influence in biomass partitioning over different developmental stages (Wang et al., 2024a). Such experiments are critically required to develop and improve mechanistic models that account for the effect of abiotic stress under a wide range of environments (precipitation and soil).

For example, the simulated root biomass could not be validated, because while there is extensive research in above-ground effects, time series data on below-ground root growth processes remains scarce. Moreover, the partitioning of assimilated carbon to different above- and below-ground components varies during growth stages and also under different stress factors. This will also impact parameterization of different models. This is further complicated by the complexity of accurately estimating below-ground biomass (Rogers et al., 1995; Madhu and Hatfield, 2013). However, emerging root phenotyping technologies can facilitate the study of below-ground processes (root growth and exudate quantification) in the coming years (Tracy et al., 2020).

Model improvement can be complex and challenging, especially if no general approaches (i.e., mathematical equations of the relationships of interest) are available. In general, there are two approaches for model improvement: (i) General approaches (e.g., the relation between biomass production and the amount of radiation absorbed by photosynthetically active tissues, see Sadras et al., 2016) are available and can be implemented as equations into the model structure; (ii) the use of experimental data that meet modelers' requirements (Kersebaum et al., 2015), which can serve for model improvement. In recent years, the Agricultural Model Intercomparison and Improvement Project (`https://agmip.org/`) consortium was created, which brings together the crop modelling community and has allowed for modelling improvement. One example is the improvement of heat stress routines in wheat crop models, which helped to reduce model uncertainty (Maiorano et al., 2017). In another example, a literature review was conducted with the aim to improve the ability of crop models to simulate heat stress impacts on wheat based on the extensive dataset of the "Hot Serial Cereal experiment" (Eyshi Rezaei et al., 2015; Webber et al., 2017).

In a similar way, to improve the overall model simulation capabilities of root:shoot biomass ratios under varying conditions, we suggest prioritizing research on the responses of root:shoot ratio to air temperature changes and N and drought stress. This will allow for a more comprehensive understanding of root:shoot ratio as affected by these factors, which can then be implemented into models. As for temperature, there are only very few and contradictory field studies on air temperature increase with respect to root responses. Moreover, drought and especially N stress have strong effects on root:shoot biomass ratios. Despite that the two latter factors are considered in the evaluated models, the responses were inconsistent.

For the current study, we focused on evaluating wheat models, due to its importance as a staple crop. However, further basic research would also be needed for underrepresented crops, as our review showed that root:shoot responses to environmental stress can vary by crop. Lastly, as the effects of CO_2 enrichment, and especially of tillage, on the mean root:shoot ratio were rather small in the case of wheat, and the simulation capabilities of the models were generally good, we consider model improvements with respect to these two factors to be less critical.

5.4 Conclusions and outlook

Process-based soil-crop models are becoming increasingly important for estimating the effects of agricultural management practices and climate change on SOC stocks. However, there is a large uncertainty in the calculation of C inputs from roots, especially under changing environmental or management conditions. Our model intercomparison study is one of the first to address root biomass simulation and root:shoot ratio. It is a first step towards identifying weaknesses for model improvement and improved understanding of effects of environmental factors on root:shoot ratio, root biomass-derived C input, and thus, simulations of SOC dynamics and carbon sequestration.

We conclude that there is a lack of time series of field experimental data on belowground processes and on the effects of major abiotic environmental stresses and tillage systems on root:shoot ratio. This is especially the case for changes in CO_2, air temperature, and drought stress. This lack of field data makes it difficult to implement general approaches that can be translated into field-scale models and proof of concepts, and it demands model improvements.

Chapter 6

General Discussion

In this discussion, insights from four complementary studies are presented to evaluate how root–shoot dynamics respond to nutrient limitations, tillage practices, and additional stresses; including drought, heat, and elevated CO_2. The second chapter synthesized field evidence on crop responses to N, P, and K deficiencies (chapter 2). The thrird chapter examined root and shoot responses of winter wheat in a two-year nutrient-omission trial within a long-term field experiment (chapter 3). The fourth chapter presented a global meta-analysis comparing no-till with conventional tillage to determine when and where tillage alters the R/S (chapter 4). Finally, the fifth chapter tested four widely used crop-soil models to simulate R/S against observed responses to nutrient stress and other abiotic drivers (chapter 5). Together, these studies offer a multi-scale perspective (from global datasets to single plots) on below-ground carbon allocation and its implications. The following sections integrate these findings, highlight their interconnections, and identify priority questions for future research.

6.1 Empirical findings consistent across studies

Table 6.1 shows the empirical findings consistent across the studies developed in this thesis and confirmed by further literature. Also, its process level interpretation is further explained.

6.1.1 Nitrogen deficiency or complete fertilizer omission reduces shoot dry matter, LAI and plant height.

The two Dikopshof seasons confirm this pattern, omitting N, or applying no fertilizer at all, lowered straw and grain yield, shoot dry matter, LAI and plant height by 20–95% compared with the fully fertilized control (chapter 3). The models in chapter 5 capture the same directional response in winter-wheat shoot biomass reported in chapter 3, although they reproduce the magnitude of the reduction under N stress less precisely. P omission mainly depresses straw biomass, while LAI and plant height remain close to the fully fertilized control (chapter 3).

N participates in protein synthesis, enzyme activity and photosynthesis. When a crop receives enough N, it grows taller and packs on more shoot biomass (Beslemes et al., 2023; Vilches-Ortega et al., 2022). If N is scarce, cell division slows, photosynthesis weakens and both plant height and shoot dry matter drop (Costa et al., 2021; Hadir et al., 2020; Liu et al., 2020a; Liang et al., 2005). LAI also falls, further reducing the plant's ability to capture light and carbon (Njuguna et al., 2016). Lower leaf area and slower metabolism leave less energy for growth, so biomass accumulates more slowly and overall vigour diminishes (Souza Miranda et al., 2010). Omitting N during key stages therefore quickly weakens shoot architecture and limits yield potential.

6.1.2 Root length and biomass decrease whenever N is deficient or no N fertilizer is applied.

Our meta-analysis of 50 field studies (chapter 2) shows that N deficiency reduces total root length by $\approx 9\%$. We observed the same trend at Dikopshof: omitting N (or withholding fertilizer altogether) cut root-length density by 20-47% across the soil profile (chapter 3).

In the global dataset, root dry mass fell by $\approx 7\%$ under N stress (chapter 2). In our field trial, N-omission and unfertilized plots carried 13-63% less root biomass than the fully fertilized control.

N shortage slows protein and nucleic-acid synthesis, so cell division and elongation in roots decline and total root biomass shrinks (Meena and Sathee, 2023; Qin et al., 2018). Plants respond with fewer branches and shorter axes because little N is available to sustain elongation (Nahar and Pan, 2015; Li et al., 2021). Primary or lateral roots may stretch briefly to forage, yet overall length still contracts as biomass shifts from growth to maintenance; an energy-saving strategy under nutrient stress (Jia et al., 2020; Sun et al., 2020; Hermans et al., 2006; Andrews et al., 1999). These shorter, less-branched systems limit the plant's ability to tap soil resources, further weakening shoot growth and yield (Chea et al., 2021; Chimungu and Lynch, 2014; Jin et al., 2024; Wang et al., 2019). When N becomes adequate, roots lengthen and branch again, restoring uptake capacity (Feng et al., 2010).

6.1.3 Compensatory fine-root proliferation under P stress.

Across the global database, SRL increased whenever soil P was scarce (chapter 2). At Dikopshof, P-deficient plots showed SRL rises of 3-48% relative to the control and a marked shift toward finer diameter classes ($> 50\%$ of the length fell below 0.15 mm), despite a 14% loss in total root length (chapter 3).

SRL typically increases and finer roots develop in response to P deficiency due to several adaptive mechanisms in plants aimed at enhancing nutrient acquisition efficiency. When P levels are low, plants adjust their root morphology to maximize surface area and improve contact with soil resources. Increased SRL indicates that roots are longer relative to their mass, allowing plants to explore a larger soil volume per unit of biomass invested (Pellerin et al., 2000; Liu, 2021; Hermans et al., 2006). This morphological change facilitates better foraging for P, which is often immobile in the soil, by forming more fine roots that can penetrate microenvironments in the soil where P might be accessible (McLachlan et al., 2019; Zhang et al., 2012). Additionally, fine roots are crucial for enhancing uptake capabilities due to a larger surface area for absorption, which becomes especially important under conditions of nutrient scarcity (Pellerin et al., 2000; Hermans et al., 2006; Zhu et al., 2010). The development of increased root hairs and finer roots has been identified as a strategic adaptation by plants to cope with P limitation, improving their ability to utilize this vital nutrient more effectively (Lynch, 2011; Wendling et al., 2016).

6.1.4 Root-to-shoot ratio under multiple stresses.

Nutrient deficiencies

The global review recorded an average 44% increase in R/S under N deficiency and a smaller but positive shift under P stress (chapter 2). In the Dikopshof experiment, R/S rose by 10-28% in N-omission plots and by 23-378% in unfertilized plots in comparison with fully fertilized treatment, whereas P omission produced no consistent response. K stress tended to decline R/S, although evidence remains sparse (chapter 2, chapter 3). Model simulations reproduced an increase of R/S under N deficiency by 1-43% (chapter 5).

When N is scarce, plants divert more sugars to their roots and slow shoot growth. This shift increases the R/S because roots are the organs that can roam the soil for extra N (Mak and Yeh, 2001; de Ferreira et al., 2015; Bacha et al., 2018; Hadir et al., 2020). Limited N also lowers photosynthesis, so leaf area and shoot biomass fall, while roots keep growing or even expand to reach a larger soil volume (Veres et al., 2018; Tolley and Mohammadi, 2020; Skinner and Comas, 2010). Experiments confirm that under N stress root growth often outpaces shoot growth, raising the R/S (Wang et al., 2016b; Zhu et al., 2021). Plants reshape their root system (more laterals, longer axes) to cope with the shortage and improve nutrient capture (Sun et al., 2016; Liu et al., 2020b). The resulting negative link between shoot biomass and the R/S underlines this trade-off: plants sacrifice top growth to secure enough N for survival (Hadir et al., 2020).

On the other hand, under K deficiency, plants often experience impaired synthesis of proteins and enzymes, leading to reduced growth rates, especially in roots. The root system, although crucial for nutrient uptake, may not be prioritized during K stress as plants reallocate resources to maintain shoot health, particularly for photosynthesis and overall vigor (Šustr et al., 2019). Studies have indicated that K deficiency can inhibit root growth activities such as elongation and lateral root development, resulting in diminished root biomass compared to shoot biomass (Thornburg et al., 2020; Šustr et al., 2019). Relatively higher biomass allocation to shoots compared to roots may ultimately lower the R/S ratio (Thornburg et al., 2020). Additionally, K is vital for osmoregulation and cellular functions in shoots, prompting plants to prioritize shoot growth under stressful conditions (Thornburg et al., 2020). Consequently, the decline in the R/S ratio reflects an adaptive strategy to ensure essential leaf functions are maintained, thereby enabling the plant to better endure periods of nutrient scarcity (Šustr et al., 2019).

Tillage

Switching from conservation to conventional tillage produced few significant R/S changes in our meta-analysis; 0.3% across all crops and 2.4% in wheat (chapter 4, chapter 5). Model outputs were likewise neutral, showing 0–8% increases (chapter 5).

Conventional tillage loosens the soil and boosts aeration but also breaks aggregates and can leave the surface prone to later compaction, limiting root exploration (Wang et al., 2015). Conservation systems (especially no-till) keep residues on the surface, preserve structure and moisture and generally support steady root and shoot growth (Busari et al., 2015). Across studies, root length density and biomass vary more with local soil conditions and tillage depth than with the tillage label itself, so root responses can look similar under different systems (You et al., 2017; Ji et al., 2013; Schneider et al., 2017). Accordingly, the R/S tends to stay much the same whether fields are ploughed, chiselled or left untouched (Anderson, 1988). Residue cover in conservation tillage conserves water and nutrients, whereas a uniform seedbed from conventional tillage can ease initial root entry but risks recompaction. These opposing effects often cancel out, leaving the overall allocation of biomass between roots and shoots broadly unchanged across tillage regimes (Chen et al., 1998; Magdoff, 1993).

Drought

Across 128 published trials, drought raised R/S by $\approx$ 14% (chapter 5, Table 5.1). When faced with drought stress, a plant's ability to absorb water becomes crucial for survival. In response, plants allocate more biomass to roots rather than shoots, which enhances their capacity to explore deeper soil layers for moisture and nutrients (Niu et al., 2008; Zhou et al., 2018; Studer et al., 2017). This increased allocation towards root growth can be attributed to enhanced root proliferation and development of finer roots and root hairs, which significantly increase the root's surface area, thereby improving water uptake efficiency (Zhou et al., 2018). Additionally, plants under drought conditions may exhibit inhibited shoot growth, leading to a decline in shoot biomass relative to roots, ultimately resulting in a higher R/S (Shamuyarira et al., 2022).

Elevated CO_2

Experiments reported a modest average R/S rise of $\approx$ 12% (5% in wheat). AgroC showed no response, and the other three models showed small changes (chapter 5). When CO_2 levels rise, photosynthetic rates typically increase, resulting in greater carbohydrate production that benefits growth (Nie et al., 2013; Rosado-Porto et al., 2021). This surplus of carbohydrates can not only facilitate the growth of shoots, but also the expansion of root systems, leading to the proliferation of finer roots (Iversen, 2009; Varga et al., 2022). Some studies have observed an increase in root biomass relative to shoot biomass, as plants reallocate resources to optimize nutrient uptake and develop a more robust root system to meet the higher demands for water and nutrients driven by increased photosynthetic activity (Cha et al., 2017; Rosado-Porto et al., 2021; Nie et al., 2013; Iversen, 2009).

Warming

Field observations point to a 20–30% drop in R/S under warming (chapter 5). Warmer air and soil speed photosynthesis and metabolic activity, so plants invest more in leaves and stems than in roots (Kandel et al., 2013). Experiments show that warming raises above-ground biomass far more than below-ground, tipping the balance toward larger shoots (Nishar et al., 2017; Salazar et al., 2019). At the same time, higher soil temperatures can weaken mycorrhizal fungi, speed up decomposition and drain nutrients, all of which limit root growth and efficiency (Qiu et al., 2021; Dukes et al., 2005; Cowles et al., 2016; Day et al., 2008). This combined effect may produce a lower R/S under warming (Wang et al., 2021; Wan et al., 2004).

Table 6.1: Convergent empirical findings. Letters in parentheses refer to the stress driver.

Trait	**Chapter 2 (meta-analysis)**	**Chapter 3 (field)**	**Chapter 4 (tillage review)**	**Chapter 5 (synthesis)**	**Agree**
Shoot biomass	N/A	↓ 20-95% (N or unfertilized)	N/A	↓ 1-40% (N)	✓
Root length	↓ 9% (N)	↓ 20-47% (N or unfertilized)	N/A	N/A	✓
Root biomass	↓ 7% (N)	↓ 13-63% (N or unfertilized)	N/A	N/A	✓
Root:shoot ratio	↑ 44% (N) ↓ (K)	↑ 10-28% (N) ↑ 23-378% (unfertilized) ↓ (K)	~0% (tillage)	↑ 64% (N wheat) ↑ 5% (tillage wheat) ↑ 21% (drought wheat) ↑ 2% (CO_2 wheat) ↓ 20-30% (warming wheat)	✓
Specific root length	↑ (P)	↑ 3-48% (P)	N/A	N/A	✓

6.2 Empirical findings varying across studies

Table 6.2 shows findings that differ across the studies presented in this thesis and, in some cases, from the literature, along with possible explanations for these discrepancies.

6.2.1 Root length and biomass under P deficiency

The meta-analysis (chapter 2) showed that P deficiency shortened root length by 14% ($n_p = 14$) and reduced root biomass by 25% ($n_p = 8$). At Dikopshof, however, only one of three sampling dates recorded a decline in root length (-77% at booting); the other two showed increases of 36% (at booting) and 65% (at flowering) relative to the control. Root biomass also behaved inconsistently: it declined early (tillering) in the season, climbed again at booting of the first growing period; however, in the second growing period, root biomass in P-stress matched the control at flowering.

One reason the Dikopshof data deviate from the meta-analysis may be the sampling timing, crop type and genotype. Most studies behind the median 14% loss in root length and 25% loss in biomass were measured only once, late in the season, after the root system had stabilized (chapter 2). At Dikopshof, roots were cored three times (tillering, booting and flowering) so the first two dates may have captured an early "transition" phase when P-starved plants produced less or more roots depending on the development stage. Variable root responses across development stages have also been reported by Steingrobe et al. (2001), who observed shifts in root growth of winter barley under P deficiency depending on developmental timing.

A second factor may be the sample size: the review's biomass estimate included only eight field studies, so its median can be skewed by a few extreme cases (chapter 2). Third, site history and soil matter. The Dikopshof plots have missed P fertilizer since 1904, yet the silty-loam Luvisol still holds residual P and ample moisture; over a century, wheat and its mycorrhiza have adapted by raising root length and mass at the end of flowering.

6.2.2 Root-to-shoot ratio under P stress

Across 50 studies (chapter 2) the R/S increased by about 9% under P deficiency, with many individual results clustering near zero. At Dikopshof the pattern was inconclusive: deficiency of P lowered the ratio by roughly 50% at tillering, raised it by about 20% at booting and left it unchanged at flowering (second growing period) in comparison with the fully fertilized treatment (chapter 3).

Several factors may explain why the meta-analysis and the Dikopshof trial did not line up on the R/S response to P stress. First, the evidence base in the review is thin. Only four field studies reported R/S under P deficiency, and their results scatter around zero, so the pooled +9% shift rests on very limited data (chapter 2). Second, developmental stage clearly influences the R/S response. Most reviewed papers measured roots near flowering/maturity, whereas in Dikopshof, root cores were taken at tillering, booting and flowering in two different growing periods. Early measurements caught an initial drop in root biomass that pushed R/S down, but by booting roots had partially recovered, and by flowering shoot mass had caught up, flattening the ratio (chapter 3).

Some studies (though few-) have also reported development stage-dependent or even increased R/S under P deficiency. For example, Duan et al. (2020) observed varying R/S responses in oilseed rape depending on developmental timing, while Hadir et al. (2020) found that P-deficient sugar beet exhibited a higher R/S ratio compared to the fertilized control. These examples support the idea that R/S plasticity under P stress may be species-specific and stage-sensitive.

Long-term site history is the third. Wheat at Dikopshof has grown without P fertilization for over a century, yet yield losses have averaged only 7–8% (Seidel et al., 2021), indicating a soil with residual P and crops that have adapted to exploit it efficiently. Such acclimation (supported by plastic, fine-rooted phenotypes and mycorrhizal associations) can reduce or even reverse the modest R/S shifts reported from shorter-term trials on other soils (chapter 3).

6.2.3 Root length and biomass response to K omission

The global evidence pointed to only minor effects of K stress on root length (chapter 2, six studies). In contrast, the Dikopshof trial showed pronounced stimulation: total root length under K omission exceeded the NPKCa control by up to 122% at flowering (chapter 3). Root-biomass data were scarce in the literature, and the field results were inconsistent; decreasing in one year and increasing in the next (in comparison with NPKCa treatment).

The mismatch between the modest, non-significant K effects in the meta-analysis and the strong root-length surge at Dikopshof can largely be traced to evidence gaps. The review drew on only six field studies and none involved winter wheat; most were short-term trials in cotton, maize, millet or soybean and generally reported small or inconsistent changes in root length, with too little information to analyze root biomass at all (chapter 2).

6.2.4 Specific root length under N stress

The meta-analysis detected little change in SRL under isolated N deficiency (chapter 2), yet the Dikopshof experiment recorded strong increases of 59% (booting) and 71% (flowering) when N was omitted (chapter 3).

The weak signal in the meta-analysis and the strong rise in SRL at Dikopshof may be explained by the evidence base. Fewer studies considered in the meta-analysis (chapter 2) reported SRL under isolated N stress, and their values clustered tightly around zero, so the pooled median may mask a tail of points showing an increase in SRL under low N. However controlled-environment studies do show that N-deficient plants commonly shift to longer, thinner roots, producing more hairs and laterals to widen their foraging zone (Yu et al., 2015; Lonhienne et al., 2014; Dresemann et al., 2018). Such plasticity is driven by reallocating carbon from thick structural tissues to exploratory tips, resulting in a higher SRL even when total biomass falls (Tian et al., 2005; Kumar et al., 2020). The Dikopshof omission plots may display exactly this classic response, whereas many field datasets in the meta-analysis (taken late in the season or on coarser soils) were less suited to detect it.

6.3 Methodological reflection: what each layer of evidence adds and where caution is still required

6.3.1 Meta-analyses as the global baseline

Meta-analyses join results from many field trials into one dataset, so they offer a wide reference for how roots and shoots react to nutrient stress and tillage before any local work begins (Berlin and Golub, 2014). Pooling studies raises statistical power and shrinks confidence bands, which helps detect small but consistent shifts that a single experiment may miss (Cuijpers et al., 2021; Murad et al., 2025). In

Table 6.2: Divergent empirical findings. Letters in parentheses refer to the stress driver.

Trait	**chapter 2 (meta-analysis)**	**chapter 3 (field)**	**Nature of the disagreement**
Root length	↓ 14% (P) ↓ slight (K)	↓ 77% (tillering), ↑ 36–65% (booting–flowering) (P) ↑ 122% (K)	Contradictory direction of change in meta-analysis vs. field.
Root biomass	↓ 25% (P) Scarce studies (K)	↓ 60% (tillering), ↑ 31% (booting), ≈ 0% (flowering) (P) ↓ one year, ↑ next (K)	Meta-analysis shows ↓ (P), field response shifts with time and year
R/S	↑ 9% (P)	↓ ≈ 50% (tillering), ↑ ≈ 20% (booting), ≈ 0% (flowering) (P)	Meta-analysis small ↑ versus stage-dependent shifts in field
SRL	≈ 0% (N)	↑ 59–71% (N)	Meta-analysis no change versus strong ↑ in field

addition, meta-analyses allow us to explore why studies differ (for example, soil texture, cultivar, sampling depth) pointing to real sources of heterogeneity rather than averaging them away (Magosi et al., 2017; Mirosevic et al., 2019).

The meta-analyses gave our research two direct benefits. First, they set the impact trait order (R/S changes more than root length, which changes more than root biomass under nutrient deficiency), so later field and modelling steps started with clear priors rather than guesses. Second, they exposed data gaps (very few K-stress trials, few tillage studies on dicot crops, and inconsistent root sampling depth) which helped the design of the following studies (Dikopshof experiment) to target one of those weak spots. In this way, the wide map from meta-analysis guided the design of local measurements.

On the other side, meta-analyses inherit all the inconsistencies of the source papers: root samples are taken to different depths, washed with different methods, and reported in different units, which extends the uncertainty in the pooled estimates (Pardi et al., 2025). Publication bias is another risk: studies with null results are less likely to appear, and this bias is not always detectable (Biljana et al., 1999). Finally, if evidence is scarce (as with K-limitation) no statistical method can fill the gap, so local data are still needed to anchor the field work.

6.3.2 Long-term field experiment at Dikopshof

The Dikopshof fertilizer experiment helped investigate more soil, shoot, and root traits (13 traits) than found in most other studies. By sampling its permanent plots during two wheat growing periods, the study traced shoot and root traits through the whole 0–100 cm profile and over three growth stages. Because the plots had received the same nutrient treatments since 1904, the observations captured slow soil changes such as P desorption that short trials rarely detect. Earlier work on long-term P omission in Dikopshof reported legacy effects on yield and soil P fractions, supporting the relevance of this site for other target traits (Seidel et al., 2021).

This method offered clear benefits for this research. Continuous management established a stable treatment legacy, ensuring consistent nutrient deficiency over time, unlike short-term experimental treatments where residual soil nutrients may persist and obscure treatment effects. Sampling paired shoot and root traits on the same plants linked below-ground change to canopy performance, an approach that earlier studies at Dikopshof had used for other nutrients and crops (Hadir et al., 2020). The Luvisol soil allowed the findings to speak to a large share of wheat land worldwide where this soil group dominates (Wanke et al., 2024).

However, the design also carried limits. Plots were not replicated due to the age of the long-term trial (established in 1904); within-plot cores were pseudo-replicates, so trait differences were reported descriptively rather than with formal tests. Regarding root sampling and processing, the position of soil core sampling is crucial, as root density is generally higher near the stem and decreases with distance. Sampling further from the stem may capture fewer roots but can provide a more representative estimate of the whole root system. Additionally, root washing procedures often result in the loss of fine lateral roots. According to Li et al. (2022), up to 25% of the actual root length can be lost during washing, which makes the absolute values conservative estimates. The work covered one site, one cultivar, two seasons and three developmental stages, so the results should be checked on other soils and genotypes before general use.

6.3.3 Model-benchmark data set for modelling

The Klein-Altendorf dataset provided the benchmark that linked our tested process-based models to measured root traits (chapter 5). Calibrating STICS, SIMPLACE, MONICA and AgroC to the same season, cultivar and soil created a common starting line for later stress-scenario runs. This single-source calibration ensured that differences seen in drought, heat or nutrient simulations came from model structure rather than from unequal tuning calibration (Wallach et al., 2021).

The approach offered several strengths for this research. The same daily weather, a layered soil profile and root biomass sampled to 1 m were used coherently as inputs instead of patchwork records (He et al., 2017). Shoot data were taken at multiple growth stages, which reduced equifinality compared with calibrations based only on yield (Specka et al., 2019).

However, the set also had clear limits. It covered only one year, one cultivar, one root sampling and one type of soil, so fitted parameter sets were non-unique and may not predict other climates or genotypes reliably (He et al., 2017). This limitation reflects a broader data gap, currently, no field data set exists that captures root responses across multiple abiotic drivers (e.g. drought, temperature, nutrient stress) under varied stress levels. In the absence of more comprehensive datasets, the Klein-Altendorf trial offered a viable baseline for evaluating model behavior across diverse stress scenarios. Additionally, stress scenarios were run "open loop," without re-tuning, so any match or mismatch remains illustrative until multi-year, multi-site data sets become available (Wallach et al., 2021).

6.3.4 What nesting scales adds to the research

By combining global overviews with detailed, long-term field experiment data from a single site, this research can compare and connect different levels of information (Table 6.3). The global data shows what we expect to happen, the long-term experiment shows what actually happens, and the models test if current theories can explain both. Using both wide and detailed approaches like this is becoming more common in agronomy and ecology.

Table 6.3: Key methodological assets and limitations

Evidence layer	**Main strengths**	**Main limitations**
Meta-analysis of nutrient stress (chapter 2)	Large n, cross-climate generality; reveals universal trait ranks	Heterogeneous protocols; K and deep-root data scarce; possible publication bias
Meta-analysis of tillage (chapter 4)	Quantifies disturbance effects independent of fertility	Few crop specific data points; short-term trials dominate
LTFE field campaign (chapter 3)	Century-long treatment legacy, full shoot–root collection, soil coring of 0–1 m profile, two growing periods	Non-replicated; root sampling limitation, root washing losses.
Model ensemble (chapter 5)	Tests process understanding; allows future scenarios	Limited root biomass data to calibrate; incomplete trait routines

6.4 Agreements and disagreements between field evidence and the crop models (Chapter 5)

In order to discuss how the four crop models generated their root-to-shoot responses, a summary of the key outcomes is presented in Table 6.4. The table pools, for every factor–scenario combination, the mean relative change (5 May – 24 June) in the simulated R/S, root biomass and shoot biomass, flags the principal driver of each ratio shift ("root-driven", "shoot-driven", "balanced", "both"), and sets these figures alongside the ranges reported in field experiments reviewed in chapter 5.

To visualize the variability behind those means, Figure 6.1, Figure 6.2 and Figure 6.3 show the same simulated daily percentage relative changes as box-and-whisker plots.

Table 6.4: Simulated root-to-shoot responses (5 May – 24 June). Values represent the average R/S across all scenarios. For each scenario group (e.g., drought scenarios 1–5), the daily values were first averaged across scenarios, followed by averaging across the studied period.

Abiotic factor	**Scenario**	**Observed relative change (%) in R/S**	**Model**	**MRC* (%) in R/S**	**MRC (%) in root biomass**	**MRC (%) in shoot biomass**	**Driver**
CO_2	enhanced	+5 (–5% to +16%)	MONICA	–1	6	7	balanced
			Simplace	–1	8	9	balanced
			STICS	0	4	4	balanced
Nitrogen	deficiency	+64 (–40% to +84%)	AgroC	0	–12	–12	both
			MONICA	11	–13	–18	shoot-driven
			Simplace	1	0	–1	balanced
			STICS	0	–38	–38	both
Precip.	drought	+21% to +27%	AgroC	–3	–37	–36	both
			MONICA	0	0	0	balanced
			Simplace	–23	–31	–9	root-driven
			STICS	0	–17	–17	both
	more precip.	n/a	AgroC	–1	1	2	balanced
			MONICA	1	–1	–1	balanced
			Simplace	3	3	0	root-driven
			STICS	0	–3	–3	balanced
Temp.	colder	n/a	AgroC	2	–57	–55	both
			MONICA	147	–35	–63	shoot-driven
			Simplace	–4	–71	–67	root-driven
			STICS	23	–60	–64	shoot-driven
	warmer	–20% to –30%	AgroC	–8	–90	–90	both
			MONICA	–35	–7	47	shoot-driven
			Simplace	8	97	96	both
			STICS	–4	–21	–17	root-driven
Tillage	higher BD	n/a	AgroC	0	–6	–6	balanced
			MONICA	0	0	0	balanced
			Simplace	0	0	0	balanced
			STICS	0	1	1	balanced
	lower BD	+2.4 (–25% to +45%)	AgroC	0	–2	–2	balanced
			MONICA	0	0	0	balanced
			Simplace	0	0	0	balanced
			STICS	0	–1	–1	balanced

Note. MRC = modelled relative change. Values are mean daily relative changes (%) with respect to each model's baseline run (scenario 6). For every factor-scenario combination the change in the R/S (Δ R/S) is attributed to one of four classes: root-driven ($|\Delta \text{ root biomass}| \gg |\Delta \text{ shoot biomass}|$), shoot-driven ($|\Delta \text{ shoot}| \gg |\Delta \text{ root}|$), balanced ($|\Delta \text{ root}| \approx |\Delta \text{ shoot}|$; difference $\leq$ 10 %), or both (large but nearly cancelling shifts in root and shoot). Positive numbers indicate an increase over the baseline; negative numbers indicate a decrease. Observed ranges quoted in the third column come from the field experiments synthesized in Chapter 5.

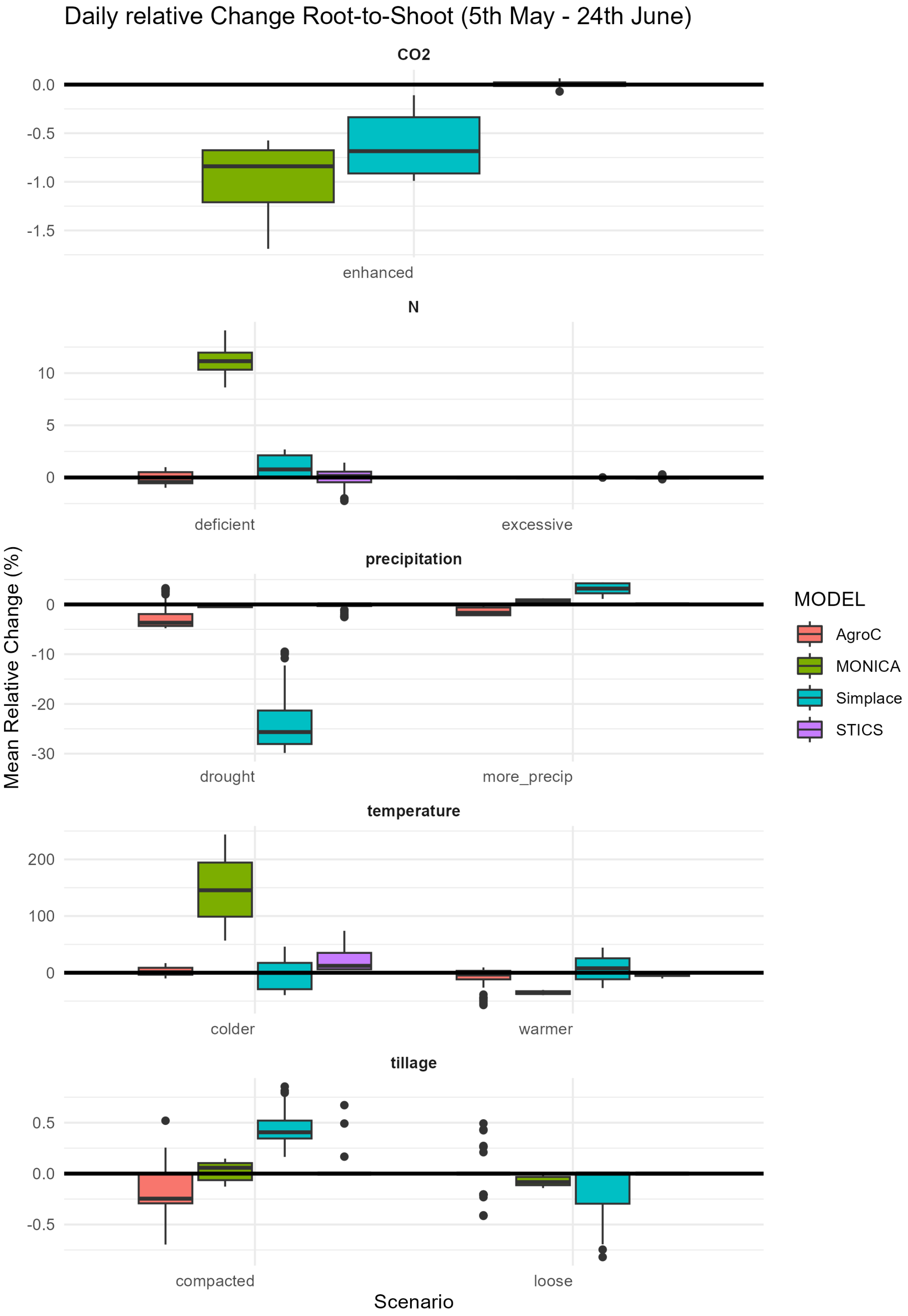

Figure 6.1: Box-and-whisker plots showing the simulated daily percentage relative changes for R/S.

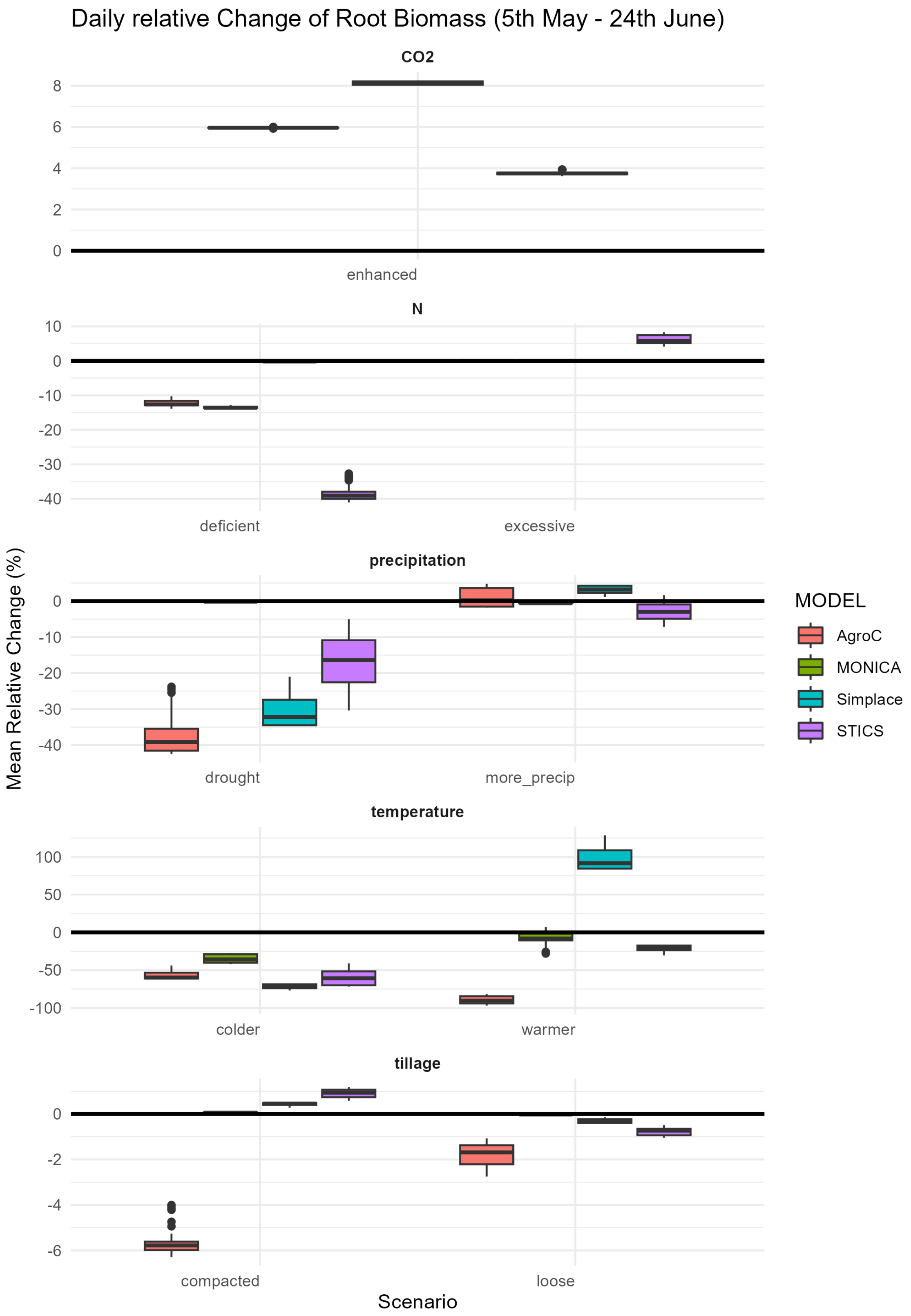

Figure 6.2: Box-and-whisker plots showing the simulated daily percentage relative changes for root biomass.

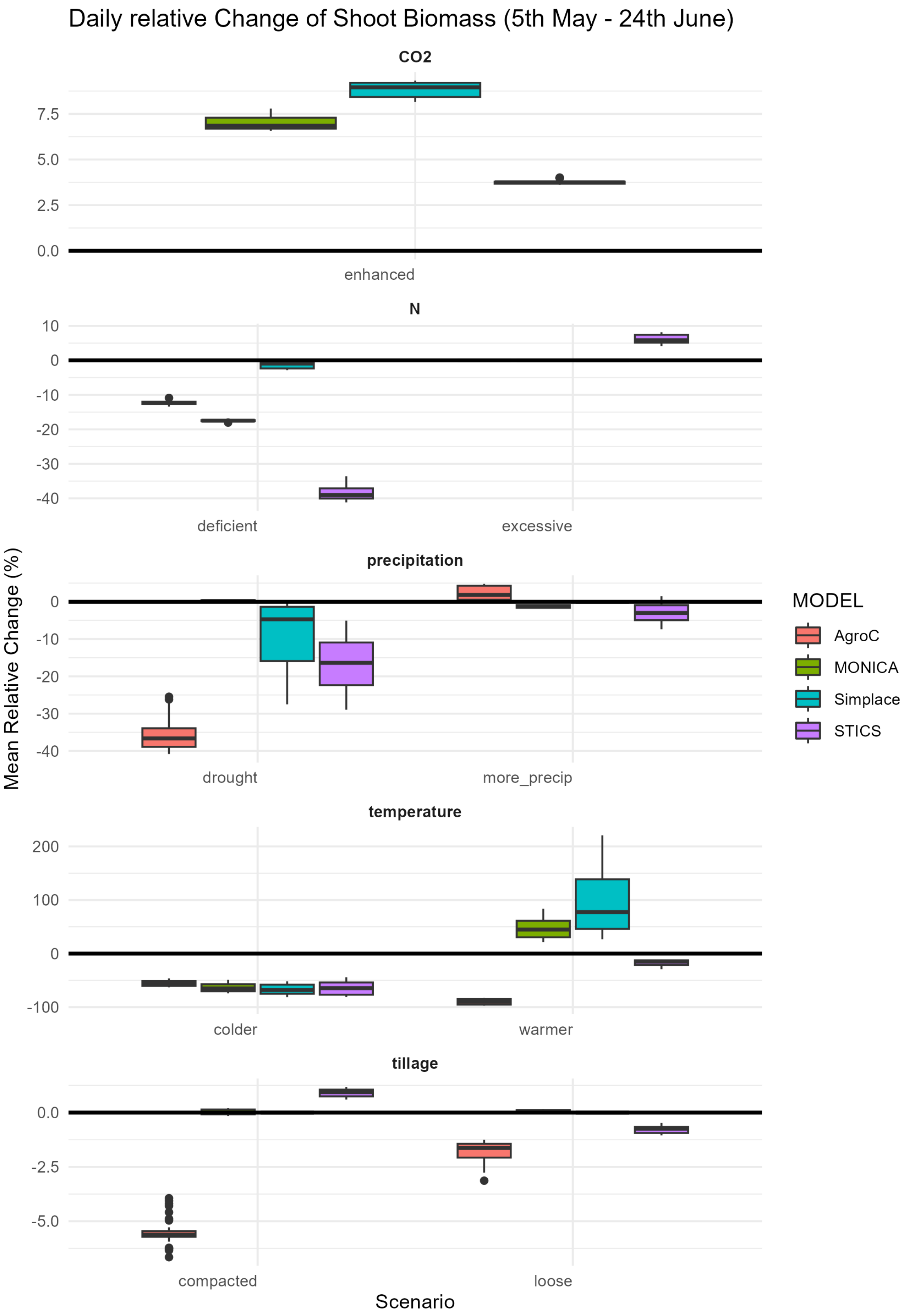

Figure 6.3: Box-and-whisker plots showing the simulated daily percentage relative changes for shoot biomass.

Understanding why the R/S changes matters because it reveals how different models allocate carbon under stress (Table 6.5). When the change is root-driven, the model tends to reallocate carbon below ground, as seen with SIMPLACE's TRANRF-based multiplier. In contrast, shoot-driven patterns, like those observed in MONICA, suggest that stress routines affect leaf and stem growth more severely than root growth. A balanced response typically indicates that the model uses fixed partitioning tables, as in AgroC, or applies equal stress scalars to both roots and shoots. All these changes can be explained due to how the four soil-crop models handle root and shoot dynamics in their routines (Table 6.6)

Table 6.5: Main drivers per tested model

Model	**Typical driver**	**Notes**
AgroC	balanced (7 / 7 cases)	Both organs usually responded in lock-step; big biomass swings under the temperature experiments and drought cancelled out in the ratio.
SIMPLACE / LINTUL-5	root-driven in 3 cases, otherwise balanced	Explicit drought-allocation rule shows up: under "drought" and "more precipitation" roots changed more strongly than shoots, shifting the ratio.
MONICA	shoot-driven (3 clear cases)	The allocation routine lets shoot mass react more than roots to N-deficit and to the cold & heat scenarios, giving large positive (cold) or negative (warm) ratio shifts.
STICS	mixed: 1 root-, 1 shoot-driven	Temperature scenarios split: colder → shoot-driven (leaf losses deeper), warmer → root-driven (roots fall off a bit faster). Otherwise root & shoot track together.

To better understand the origins of the simulated changes, Table 6.7 examines which responses can be directly attributed to specific model algorithms and which remain ambiguous or cannot be clearly traced.

Based on that analysis, for future work we could choose the model depending on the stress type:

- **Drought or soil-water deficit.** The only platform that simulates a realistic shift of assimilate below-ground is SIMPLACE / LINTUL-5: its FRTMOD multiplier raises the root fraction whenever the transpiration-reduction factor (TRANRF) drops below 0.5. STICS, AgroC and MONICA should be used with caution; STICS has the water-allocation link switched off for wheat, while AgroC and MONICA leave allocation unchanged (MONICA merely deepens the rooting depth).
- **Nitrogen deficiency (or excess).** For N-stress studies the most suitable choice is MONICA, whose dedicated N-stress functions (Eqs. S12–S13) scale root and shoot growth differently and can shift the ratio in line with field observations. AgroC, SIMPLACE and the default STICS crop file should be avoided: AgroC relies on a fixed partitioning table, SIMPLACE pushes surplus C into stems so the ratio rises by only a few percent, and the N-REPRAC coupling is disabled in the supplied STICS configuration.

Table 6.6: Different ways how the models handle the abiotic stresses

Dimension	SIMPLACE / LINTUL-5	STICS (v10)	AgroC	MONICA
Partitioning rule in baseline (no stress)	Daily biomass is split with fixed root, stem, leaf fractions that vary with development stage (DVS table).	Root-to-total coefficient REPRAC varies continuously with the temperature-driven root development unit URAC; colder weather raises the ratio [Eq. S10].	Fraction to shoot (FSH) is read from a DVS lookup table; remainder goes to roots, so the ratio is essentially fixed by phenology.	Assimilates from a Farquhar-type photosynthesis routine are distributed to roots, leaves, stems and grain with crop-stage-specific coefficients; the ratio is calculated afterwards.
Drought response	If the transpiration reduction factor TRANRF < 0.5, a multiplier (FRTMOD) boosts the root fraction; shoot fractions shrink proportionally [Eq. S7].	Water stress can down-regulate REPRAC, but this option is off for winter wheat in v10.	No effect; the DVS table is unchanged, so only indirect temperature effects appear.	No change in C allocation; instead the maximum rooting depth expands under drought.
Nitrogen stress	Leaf fraction is reduced by FLVMOD when the N Nutrition Index drops; excess C moves to stems, giving only a small rise in the ratio ($\leq$ 3%).	N can couple with REPRAC, but the link is disabled for wheat in the current configuration.	Not represented; the table remains fixed, so simulated ratio change scatter around 0.	N-stress factor (Eq. S12–S13) scales root and shoot growth differently, giving the strongest ratio response of the four models ($\approx$ 20-50% across scenarios).
Temperature & CO_2 effects	RUE modifiers adjust total assimilation; allocation responds indirectly plus FRTMOD/FLVMOD if stresses emerge.	URAC is temperature-driven, so warmer days lower the ratio; CO_2 alters RUE but not partitioning directly.	Temperature shifts phenology and therefore the table look-up.	Temperature influences development rate and photosynthesis; allocation coefficients are stage-specific but fixed with respect to CO_2.
Bulk density	SlimRoots module limits elongation with soil strength and accounts for macropores.	Bulk-density thresholds.	No explicit mechanics; only hydraulic feedback via Richards equation on water uptake. Explicit root exudation routine.	Root length distribution rule; depth increases exponentially with thermal time.

Note. The references to equations can be found in the supplementary material of chapter 5.

Table 6.7: Agreement between model structure and field evidence across stress scenarios

Abiotic factor & scenario	**Agreement between mechanism and modelled R/S change**	**Fits the field evidence?**	**Remarks**
CO_2 enrichment	All models show 0-1 % because none includes the CO_2 directly in its partitioning rules; exactly what their designs predict.	Partly. Field meta-analysis points to a +5 % median rise.	Without a direct allocation response, the models cannot reproduce the observed shift accurately.
N deficiency	MONICA (+11 %, shoot-driven) is explainable: its N-stress factors scale shoot growth more strongly than root growth. AgroC, SIMPLACE, STICS ∼ 0 % because they rely on fixed (or disabled) partitioning tables or the effect is cancel.	Partly. MONICA lands in the observational range (–40 % to +84 %); the others greatly underestimate it.	Capturing the empirical plasticity requires a model that differentiates N stress between organs; only MONICA does.
Drought	AgroC, MONICA, STICS ∼ 0 %: predictable (no allocation rule). SIMPLACE should raise R/S via FRTMOD, but it instead falls (–23 %, root-driven) → not explained by its documentation.	No. Observed change is +21–27 %.	Only SIMPLACE contains an explicit drought-allocation routine, yet its sign is opposite; the other three miss the effect by design.
Extra precipitation	SIMPLACE (+3 %, root-driven) matches its rule that relaxes FRTMOD when water is non-limiting. Other models ±1 % as expected.	n/a (no field benchmark).	Mechanistic behaviour is internally consistent.
Colder season	STICS (+23 %, shoot-driven) aligns with its URAC formula that raises R/S under low temperature. AgroC (+2 %) and SIMPLACE (–4 %) small by design; MONICA huge jump (+147 %) unexplained (allocation is fixed).	n/a	STICS behaves as designed; MONICA's extreme shift suggests secondary interactions.
Warmer season	STICS (–4 %, root-driven) and MONICA (–35 %, shoot-driven) move the ratio down; the sign expected from faster phenology or heat stress. AgroC (–8 %) and SIMPLACE (+8 %) have no explicit heat rule.	MONICA is close to the observed –20 % → –30 % window.	Only MONICA achieves field-like magnitude, but it does so without an explicit partitioning routine; an acceptable but indirect match.
Lower bulk density	SIMPLACE & STICS contain soil-strength limits yet produce ∼ 0 % shifts—not explained by their impedance routines (perhaps change in BD was mild). AgroC & MONICA 0 % as expected.	Observed median +2.4 %; models miss but the range is wide (–25 % to +45 %).	Mechanical-impedance code did not trigger under the scenario settings used.

- **Temperature (cold or heat).** STICS is preferred because its root-to-total coefficient (REPRAC) varies continuously with the temperature-driven root-development unit (URAC): colder weather raises, hotter weather lowers the ratio in line with field data. AgroC and MONICA hold stage-specific but fixed coefficients, and SIMPLACE alters allocation only indirectly via stress multipliers triggered by water or N shortages, so these three should be used only with caution.

- **Elevated CO_2.** None of the four models is fully adequate for partitioning work under CO_2 enrichment. All adjust photosynthesis or radiation-use efficiency, but their allocation coefficients are fixed with respect to CO_2. These models could be use only when total biomass is the target, not partitioning (or apply an empirical correction outside the model.

- **Soil compaction or tillage.** When mechanical impedance is the question, choose SIMPLACE or STICS. Both constrain root elongation in response to bulk density (SlimRoots in SIMPLACE, Jones-type thresholds in STICS), allowing root biomass and the R/S ratio to react. AgroC and MONICA lack a soil-strength routine and simulate only hydraulic feedback, so they are unsuitable here.

- **Rhizodeposition / below-ground C inputs.** Only AgroC carries an explicit root-exudation routine (Eq. S11) linked to root growth and is therefore the sole option when carbon fluxes to the soil are required. SIMPLACE, STICS and MONICA do not simulate rhizodeposition.

Future work should prioritize aligning documented algorithms with simulated patterns to ensure interpretability of model behavior. When simulation results diverge from observations but are consistent with the model's structure, the mismatch can be explained and attributed to inherent model limitations. However, when outputs contradict the underlying algorithms or when key processes are absent altogether, these discrepancies highlight critical areas for code inspection or parameter refinement. Addressing these gaps is essential before applying the model to simulate responses under specific stress conditions.

6.5 Implications for management and breeding

The following management implications and breeding priorities are derived from the evidence presented in this research. Together, the findings show that integrated practices (including nutrient supply optimization, conservation tillage) can support more carbon from roots which can later translate into carbon sequestration.

- **Match N supply to crop demand.** Field trials at Dikopshof showed 30-60% yield loss and decrease in root biomass when N was fully withheld (chapter 2 and chapter 3) and a global survey reported similar penalties under N stress (Tolley and Mohammadi, 2020). This shows the importance of matching N supply to crop demand. However, there are efficient ways to do so, split-N meta-analysis found 7% higher yield and lower leaching in cereals (Hu et al., 2021; Singh et al., 2024). Delaying or splitting the first N top-dress until soil mineral-N falls below about 40 kg ha^{-1} can hold winter-wheat grain and protein while cutting nitrate leaching and nitrous-oxide losses. For farmers, this practice reduces early fertilizer cost; for the environment it lowers reactive-N escape, and for crops it avoids early luxury uptake that later depresses root growth.

- **Mobilize legacy soil P before applying new inputs.** Grain at Dikopshof fell only 7% after nearly a century without P because Olsen-P stayed above 15 mg kg^{-1} (chapter 3, (Seidel et al., 2021; Wang et al., 2016a)); long-term European studies reported similar safety margins at that threshold (Bollons and Barraclough, 1999; Colomb et al., 2007; Mallarino and Blackmer, 1992). Pausing P fertilizer on fields exceeding this level could reduce P inputs by up to half without harming yields. In fact, P omission increased SRL at Dikopshof (chapter 3), and high SRL is associated with improved P uptake in wheat (Deng et al., 2018). Although P and K are typically applied in autumn at Dikopshof, assuming low mobility, some P-sensitive crops (such as maize) often receive NP or NPK fertilization in spring to meet early-stage demand. By exploiting residual soil P and supporting root traits that enhance acquisition, farmers can maintain productivity, lower fertilizer costs, and reduce P runoff to surface waters.

- **Recycle manure or compost to build soil carbon and foster deep rooting.** At Dikopshof, combining manure with mineral fertilizer increased root length by 60% in the topsoil (chapter 3). Long-term experiments on loess soils have shown that continuous manure application contributes an additional 0.3–0.6 t C ha^{-1} yr^{-1} to SOC when combined with mineral nutrients (Abdalla et al., 2022; Das et al., 2023). Enhanced SOC improves water retention, supports deeper rooting, and reduces erosion risk. Although manure spreading involves added labor and costs, it can offset mineral fertilizer needs and may qualify for carbon credit schemes.

- **Adopt shallow non-inversion tillage to raise SOC without yield loss.** A tillage synthesis in wheat recorded stable yield and an average SOC gain of 0.46 t C ha^{-1} yr^{-1} when mouldboard ploughing was replaced by shallow non-inversion (Liu et al., 2023). Meta-analysis in chapter 4 and models in chapter 5 echoed the minimal change in R/S ratio under NT and CT, so root supply is unlikely to fall. Less inversion lowers diesel use and CO_2 emissions while conserving soil moisture through surface residue.

- **Mitigate drought with deep-rooting, high-SRL cultivars plus residue cover.** Both the meta-analysis and Dikopshof data showed drought and low N raised R/S by about 15–40% (chapter 2, chapter 3 and chapter 4). Deep-rooted wheat lines captured more nitrate below 1 m and maintained yield in dry seasons (Odone et al., 2024). Surface mulch further reduced evaporation on loess soils (Liao et al., 2021). For crops the combination secures grain and improves water uptake; for the environment it trims nitrate leaching; for farmers it mitigates income against drought years.

- **Breeding focus on root plasticity and depth.** A key focus for breeding should be on enhancing root plasticity and depth, as these traits are strongly associated with improved nutrient acquisition and stress tolerance. High SRL under P deficiency has emerged as a particularly valuable trait. In chapter 3, SRL increased under P omission, and external studies further support the link between elevated SRL and enhanced P acquisition.

  N stress also revealed important root-shoot allocation dynamics. Genotypes that showed greater flexibility in biomass allocation (shifting more carbon belowground) were able to maintain higher overall biomass in low-N plots, as observed in chapter 2 and chapter 3. Additionally, studies showed significant variation among genotypes in response to N stress, with root allocation differing by as much as 35% (Tolley and Mohammadi, 2020).

  The development of deep axial roots represents another promising trait. These roots have been associated with increased uptake of deep soil N and improved drought tolerance, as demonstrated in recent multi-genotype field experiments (Odone et al., 2024).

6.6 Future work

Based on the gaps found in this research, the following studies may be conducted to improve the relevant understanding:

- **Run multi-site, multi-year, high temporal resolution nutrient-omission trials that include full (at least 0–100 cm) root profiles.** Most long-term experiments, including Dikopshof, sample one site and two or three growth stages; deep soil and coarse textures are under-represented. Multi-site data would test whether the large N-penalties seen on Luvisols also appear on sandy or clay soils and would give better calibration points for carbon models (Burger et al., 2024). Root coring to 100 cm or minirhizotron imaging at several depths should be paired with seasonal N and P budgets to link allocation to uptake.
- **Establish field warming plots that track R/S and SRL.** Field measurements of root response to +3-5°C are scarce and contradictory; chapter 5 showed that model spread was widest for heat scenarios. Warming experiment in wheat, combined with coring and minirhizotron tubes, would give direct data on how warming shifts allocation and depth distribution (Hou et al., 2018).
- **Quantify K effects on root traits under contrasting moisture.** Only five field studies reported K-stress effects in the meta-analysis (chapter 2) and the findings in Dikopshof were not conclusive (chapter 3). K shortage often co-occurs with drought and may trigger compensatory rooting. Factorial K × water experiments could help to understand the changes in shoot biomass, root biomass, root length, diameter classes and R/S under these stresses.

- **Measure in-situ root exudation together with morphology.** Carbon input from exudates is missing in this research. New in-situ trapping and ^{13}C-pulse methods can give hourly exudation rates while retaining the root sample for trait analysis (Wang et al., 2013; Zhang et al., 2024b). Coupling these data to soil-C pools will improve sequestration estimates.
- **Calibrate models with higher temporal resolution and stress-specific datasets.** The Klein-Altendorf baseline data was scarce in root biomass. Future calibrations ideally should include higher temporal resolution, drought, low-N and warming seasons at the same site, then validate at independent sites in order to run more reliable scenarios. Furthermore, adding explicit routines for the testing scenarios and root exudate modules, which exist in prototype form, would let models test fine-root dynamics rather than infer them indirectly (Arnhold et al., 2024; Wang et al., 2013).
- **Track deep-root carbon inputs under reduced tillage.** The tillage review showed mainly root allocation at the topsoil but root inputs below 50 cm remain scarce. Core sequencing of ^{14}C or δ^{13}C profiles in paired plough vs. no-till plots, combined with biomass measurements, would verify whether deeper roots actually increase sub-soil carbon stocks (Burger et al., 2024).

6.7 Conclusions

This thesis examined root-shoot dynamics under nutrient limitations, tillage practices, and abiotic stresses using meta-analyses, long-term field experiments, and crop-soil models. N deficiency consistently reduced shoot and root growth and increased R/S, while P deficiency induced complex and variable root responses, with increased SRL. Tillage practices showed minimal impact on R/S. Abiotic stresses had distinct effects: drought and elevated CO_2 increased R/S, while warming reduced it due to enhanced shoot investment. Although crop models captured some general trends, they often underestimated the magnitude of responses under certain stresses or failed to reproduce others altogether, highlighting the need for more accurate representation of root processes. Overall, the thesis highlights root–shoot coordination as key to plant adaptation and calls for better modeling and field methodologies to support sustainable agriculture.

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Supplementary Material

Appendix A

Supplementary material for chapter 2

Table A.1: Effects of N deficiency and different N application levels on root morphology and root distribution as well as on root biomass. Treatment description: N0 stands for no N fertilizer applied, N(N supply level) stands for the amount of N applied in kg ha^{-1} (e.g. N150: 150 kg N ha^{-1} were applied). A detailed bibliography of the references is included in the main manuscript.

Crop, Site, Soil	**Treatments and Sampling**	**Effects on Root Morphology and Distribution**	**Effect on Root Biomass and Root-to-Shoot Ratio**	**Reference**
Crop: Maize. Site: USA, 3 yrs. Soil: silt loam.	Two N rates: N0 and 180 kg N ha^{-1} (N0 and N180). Root sampling: At ~9, 12 and 19 weeks after planting. Root coring (0–0.6 m). Root length by counting intersections on a grid. Root diameter using a dissecting microscope.	Lower root length at N0 compared to N180 in 2 of 3 years. N0 increased root radius in all three years.	Decreased root weight without N fertilization in the 0–0.07 m soil layer in one year but slightly increased (not significant) in two years. Root mass per length decreased with N fertilization. Significant increases of the root-to-shoot ratio (0.26–0.40) and root-N-to-shoot-N ratio (0.61–0.84) at N0 in all 3 years.	(Anderson, 1987, 1988)
Crop: Maize (two genotypes). Site: USA. Soil: silt loam (two field sites).	Two N levels: N0 and 227 kg N ha^{-1} (N0 and N227). Root sampling: At 31, 47, 75 and 91 days after planting. Coring from row and 35 cm from row. Root length measured by the root-intersect method.	Percentage of roots with root hairs was not affected by N application. N application increased both length and density of root hairs in both genotypes. Root length was higher at N227 for one cultivar but similar for the other compared to N0. N application increased root growth rate in the topsoil during the early vegetative stage.		(Barber and Mackay, 1986)
Crop: Winter Wheat. Site: England. Soil: silty clay loam.	N fertilizer rates: 0 and 154 kg N ha^{-1} (N0, N154). Two water-supply levels: irrigated and drought.	N fertilizer increased root lengths by 32 % overall; drought reduced root length by 14%.	Three treatments had little effect on total root dry weight (116–134 g m^{-2} at anthesis), but the drought + low-N crop was significantly lower (97 g m^{-2}). Low N supply increased the root-to-shoot weight ratio.	(Barraclough et al., 1989)

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Table A.1 – continued from previous page

Crop, Site, Soil	**Treatments and Sampling**	**Effects on Root Morphology and Distribution**	**Effect on Root Biomass and Root-to-Shoot Ratio**	**Reference**
Crop: Cotton. Site: China. Soil: loam.	N rates: 0, 120, 240, and 480 kg N ha^{-1} (N0, N120, N240, N480). Root sampling: Canal drill (d=70 mm, 150 cm depth) in 15 cm layers. Scanned and analyzed with WinRHIZO.	A moderate N rate (240 kg ha^{-1}) increased root length, root surface area and root biomass in most soil layers; total root growth and root biomass increased by >36.06% relative to N0. Surface-layer roots were more affected by N fertilization than deeper roots.		(Chen et al., 2020a)
Crop: Spring Wheat. Site: UK (two sites). Soil: silt loam, clay loam.	N rates: 0, 67, and 134 kg N ha^{-1} (N0, N67, N134). Sites: Crookston and Morris. Root sampling: Hydraulic probe (d=6.6 cm) centered between rows.	Root length was affected by N rate at both years and sites. 67 kg ha^{-1} stimulated root growth in the top 30 cm. 134 kg ha^{-1} caused no change or a decline in root length. Genotypes reacted differently to N fertilization, especially in surface layers (1982). Root growth was modified by local climate and soil types. Since forage production was similar at 67 and 134 kg ha^{-1}, the decline in total root growth at 134 kg ha^{-1} may explain differences in water use.		(Comfort et al., 1988)
Crop: Maize (three genotypes). Site: USA. Soil: Silty clay loam (Typic Argiudoll).	N rates: 0, 60, 120, 180 kg N ha^{-1} (N0, N60, N120, N180). Root sampling: At tasseling; soil cores (0–0.9 m), washed, sieved, dried.	Root dry weight, length and root-to-shoot ratio decreased linearly as N rate increased. Genotypic differences in root dry weight, radius, and root-to-shoot ratio were observed.	At N0: root dry weight = 26.3 g plant^{-1} (vs. 25, 19, 20 g at N60, N120, N180). Root-to-shoot ratio increased at N0 (0.193) vs. (0.159, 0.128, 0.145) at N60, N120, N180.	(Eghball and Maranville, 1993)

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Table A.1 – continued from previous page

Crop, Site, Soil	**Treatments and Sampling**	**Effects on Root Morphology and Distribution**	**Effect on Root Biomass and Root-to-Shoot Ratio**	**Reference**
Crop: Maize. Site: China. Soil: medium loam.	N rates: 0, 90, 180, 270 kg N ha^{-1} (N0, N90, N180, N270). Split-plot: biodegradable film vs. polyethylene film. Root sampling: Soil cores (15 × 15 × 10 cm) at 10 cm intervals (1–40 cm); WinRHIZO analysis.	Compared to N0, N application increased root-length density (0–20 cm), root-surface-area density (0–10 cm), root weight (0–10 cm), and root-to-shoot ratio by 41.6%, 38.8%, 89.8%, and 33.0% (biodegradable film), and by 40.3%, 33.9%, 61.5%, and 23.3% (polyethylene film).		(Fang et al., 2022)
Crop: Maize. Site: China (3 yrs). Soil: loamy clay, clay loam, sandy loam.	N rates: 0, 168, 240, 270, 312 kg N ha^{-1} (N0, N168, N240, N270, N312). Root sampling: Soil cores to 0.6 m at silking; washing, sieving, scanning.	In loamy clay and clay loam, total root length increased with N up to 168–240 kg ha^{-1}, then decreased at higher N. In sandy loam, no relationship between N and total root length was found.	Root biomass at silking was affected by site and year, but not by N rate. Root-to-shoot ratio at silking was unaffected by N rate.	(Feng et al., 2016)
Crop: Sugar Beet. Site: Germany [1]. Soil: Silty loam.	N treatments: N0; 160 kg N ha^{-1} + manure (N160); and 80 kg N ha^{-1} (N80), long-term. Root sampling: 38, 66, 93, 155 days after sowing; shovel excavations (topsoil); WinRHIZO.	Total root length and root diameter increased with N level on all sampling dates. At date 1: root diameter = 0.46, 0.44, 0.41 mm for N0, N80, N160; on dates 2–3, N0 had lower diameter than N80, N160.	At dates 1–2: root dry matter was lower in N0 vs. N80; at dates 3–4: higher in N0; N160 had greatest root dry matter. Root-to-shoot ratio at N0 was highest on 3 of 4 dates (last date: 5 vs. 4 vs. 3.3 for N0, N80, N160).	(Hadir et al., 2021)
Crop: Winter Oilseed Rape (3 cultivars). Site: Belgium. Soil: Luvisol.	N rates: 0 and 240 kg N ha^{-1} (N0, N240). Root sampling: Tube-rhizotron (1 m tubes at 45° to ∼48 cm depth); BBCH stages 15, 18, 19, 55, 65, 75, 89; Optimas v6.1.	At BBCH 18: root-length surface density (36–48 cm) was higher at N0 than N240. High heterogeneity between rhizotron images; no obvious cultivar differences in rooting depth or placement.		(Louvieaux et al., 2018)

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[1] Long-term field experiment since 1904. Silty loam (topsoil) and (silty) clay loam (subsoil).

Table A.1 – continued from previous page

Crop, Site, Soil	**Treatments and Sampling**	**Effects on Root Morphology and Distribution**	**Effect on Root Biomass and Root-to-Shoot Ratio**	**Reference**
Crop: Maize (two genotypes). Site: USA. Soil: silt loam (Raub and Chalmers).	N rates: 0 and 227 kg N ha^{-1} (N0, N227). Root sampling: 31, 47, 61, 75, 91, 109 days after planting; coring at row and 35 cm from row; root-intersect method.	Total root length increased under N227 for Pioneer 3732, but was similar in B73×Mo17. B73×Mo17 had greater root growth in fertilized topsoil (0–25 cm). N0 increased root length in one genotype but not the other.		(Mackay and Barber, 1986)
Crop: Winter Wheat. Site: Iran. Soil: (unspecified).	N rates: 0, 150, 300 kg N ha^{-1} (N0, N150, N300) in 2015/16, 2016/17. Irrigation: furrow (OFI) vs. alternate furrow (VAFI). Planting: on-ridge (ORP) vs. in-furrow (IFP). Root sampling: 0–0.8 m with 1 m × 0.05 m diameter auger; GiaRoots analysis.	N fertilization increased mean RLD vs. unfertilized. N150 showed higher root density in 0–30 cm and less deep penetration vs. unfertilized; N150, N300 differed from N0 but not from each other.	N application increased RMD vs. unfertilized. In Year 1, N increased RMD by 32%; in Year 2, by 5%.	(Mehrabi et al., 2021)
Crop: Sorghum. Site: Australia. Soil: Tindall clay loam.	N rates: 0 and 100 kg N ha^{-1} (N0, N100). Hybrids: Texas 610, Pioneer 846. Root sampling: 5 cm auger; 0–150 cm in 10 cm layers; line-intersect method.		No significant differences in total root dry matter; all treatments ∼1000 kg ha^{-1} except Texas 610 at N0 (∼600 kg ha^{-1}).	(Myers, 1980)
Crop: Sorghum. Site: India. Soil: (unspecified).	N rates: 0 and 100 kg N ha^{-1} (N0, N100) in 1996 rainy season. Varieties: CSH9, FSRP. Root sampling: 60 cm monolith; COMAIR root scanner.	Root length was not greatly affected by N in both hybrid and local variety. N uptake in local variety at 100 kg ha^{-1} remained constant after booting.	Root dry mass increased with N fertilization.	(Nakamura et al., 2002)
Crop: Maize. Site: USA. Soil: silt loam.	N rates: 0 and 168 kg N ha^{-1} (N0, N168). Tillage: conventional vs. no-tillage. Root sampling: auger (0–90 cm) on four dates; line-intersect method.	Under conventional tillage, N0 showed increased total root length (0–90 cm) across the season. Under no-tillage, N0 vs. N168 difference was significant only at flowering.		(NaNagara et al., 1976)

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Crop, Site, Soil	**Treatments and Sampling**	**Effects on Root Morphology and Distribution**	**Effect on Root Biomass and Root-to-Shoot Ratio**	**Reference**
Crop: Sugarcane. Site: Brazil (2 sites). Soil: Typic Kandiudox (TK), Rhodic Eutrudox (RE).	N treatments [2]: N0, N120 (plant cane); N0, N150 (ratoon). Root sampling: Ratoon cycle: 125, 145, 211, 225, 274, 288, 349, 369 days after harvest; coring to 0.6 m.	At TK: N increased root density later in cycle.	At RE: N increased root-to-shoot ratio early in cycle; later similar to control.	(Otto et al., 2014)
Crop: Maize. Site: China (3 yrs). Soil: silt loam.	N treatments: N0; N at and after tasseling 250 kg ha^{-1} (TDAT); N before tasseling 250 kg ha^{-1} (TDBT); 450 kg ha^{-1}. Root sampling: 40, 57, 74, 103, 130, 148 days after sowing; auger (0–50/60 cm), washing, root-length analysis.	N0 stimulated root growth early (V8 stage). Total root length peaked before tasseling, then declined earlier than treatments with base N or TDBT. N0 enhanced embryonic root growth before V12 but suppressed nodal root initiation and growth (especially 7th whorl) after tasseling.	(—)	(Peng et al., 2012)
Crop: Cotton. Site: Georgia, USA (long-term experiment). Soil: sandy loam.	N rates: 0, 60–65, 120–130 kg ha^{-1} (N0, N60, N120). Tillage: no-till (NT), chisel till (CT), mouldboard till (MT). Root sampling: 0–120 cm by hydraulic probe (d=5 cm, L=120 cm) in layers 0–15, 15–30, 30–60, 60–90, 90–120 cm.		Total aboveground biomass at 15 cm depth was greater in CT+N60 than NT+N120. Root biomass showed no significant differences among treatments; significant tillage×fertilization interaction observed.	(Sainju et al., 2005)

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[2] Four N treatments: 0 and 120 kg N ha^{-1} at sowing, and after the first harvest (4 months) 0 and 150 kg ha^{-1} N (treatments: 0–0, 0–150, 120–0, and 120–150). Root sampling: Coring near the place of biomass collection, 0.3 m and 0.6 m apart from that

Table A.1 – continued from previous page

Crop, Site, Soil	Treatments and Sampling	Effects on Root Morphology and Distribution	Effect on Root Biomass and Root-to-Shoot Ratio	Reference
Crop: Maize. Site: USA. Soil: silt loam, clay loam.	N rates: 0 and 157 kg ha^{-1} (N0, N157). Root sampling: Cores (60 cm d=5 cm) in 10 cm layers; WinRHIZO.	Fewer nodal roots correlated with greater shoot mass under N stress. Lines with fewer, thicker nodal roots had higher dry shoot biomass under low N than lines with many, thin nodal roots. The "few, thick nodal root" phenotype was associated with deeper root distribution and improved shoot growth under N stress.		(Schneider et al., 2020)
Crop: Potato (two genotypes). Site: Canada. Soil: (unspecified).	N rates: 0 and 150 kg ha^{-1} (N0, N150). Root sampling: 54, 76, 96 days after sowing; cores 0–15, 15–30 cm; washing, digital imaging, WinRHIZO; drying, weighing.	Root length and RLD did not differ significantly between N treatments.	Higher tuber fresh weight at N150 vs. N0 in third sampling. Root-to-shoot ratio was higher at N0 vs. N150.	(Sharifi et al., 2005)
Crop: Maize. Site: New Zealand. Soil: fine sandy loam.	N rates: 0, 168, 672 kg ha^{-1} (N0, N168, N672). Root sampling: Wire-netting containers (20 × 51 cm) to 91 cm; one plant/container; harvest 0–90 cm at 69, 127, 189 days after sowing; dry, weigh.		At early stage: root dry weight at N0 (14 g plant^{-1}) vs. N168 (8 g), N672 (12 g). At grain fill: N0 (26 g) vs. N168 (21 g), N672 (21 g).	(Thom and Watkin, 1978)
Crop: Wheat. Site: China. Soil: loamy (2 sites), clay (1 site).	Site 1–2: N0, N180, N360 kg ha^{-1}. Site 3: N0, N180, N240, N360. Irrigation: no-irrigation (W0), irrigated at jointing+booting (W2; 750 m^3 ha^{-1} each). Root sampling: Soil blocks (30×30×60 cm); washing, WinRHIZO.	Kaifeng: N180 had highest RWDV in 0–20, 20–40, 40–60 cm (both seasons). Zhengzhou, Wenxian (W2): N180 highest RWDV in 0–20 cm; N0 highest in 60–80, 80–100 cm.	Under irrigation (W2), N180 yielded max RWDV (0–100 cm); under W0, N0 had max RWDV, declining with increased N. Both W0 and N0 increased R/S, with W0N0 highest. Irrigation and N significantly impacted RWDV; under W2 (2012–13), N180 had highest 0–100 cm RWDV. Under W0, N0 had highest RWDV, decreasing with N rate.	(Wang et al., 2014)

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Crop, Site, Soil	**Treatments and Sampling**	**Effects on Root Morphology and Distribution**	**Effect on Root Biomass and Root-to-Shoot Ratio**	**Reference**
Crop: Barley. Site: England. Soil: (not provided).	N rates: 0, 50, 100, 150 kg ha^{-1} (N0, N50, N100, N150). Root sampling: Cores to 0.8 m; harvested at 46, 60, 74, 95, 130 days after sowing; washing, drying, weigh.	N up to 100 kg ha^{-1} increased total root weight, mainly in 0–15 cm. Root-to-shoot ratio higher at N0, N50 vs. N100, N150 (e.g., D5: 0.09 vs. 0.07). N0 had highest R/S at earliest stage.	N increased shoot more than root, thus decreasing R/S.	(Welbank and Williams, 1968)
Crop: Winter Wheat. Site: China. Soil: (unspecified).	N rates: 0, 122, 174, 300 kg ha^{-1} (N0, N122, N174, N300). Root sampling: 30×30×60 cm blocks; washing, digital imaging, software.	At jointing: N0→N174 significantly increased RLD, RSA in 0–30, 30–60 cm; N122 intermediate. N174→N300 had no effect. At flowering: similar effects but less pronounced. At maturity: N0→N174 increased RLD, RSA in 0–30, 0–60 cm; N174→N300 similar.	Compared to N0: N122, N174 significantly increased root dry weight (0–60 cm) at anthesis; N174→N300 slight decline. Root DW (30–60 cm) unaffected by N at anthesis. At maturity: N supply increased root DW (significant N150, N300).	(Xue et al., 2014)
Crop: Rice (two hybrids). Site: China. Soil: clay loam.	N rates: 0, 60, 120, 180 kg ha^{-1} (N0, N60, N120, N180). P rates: 0, 60, 90, 120 kg ha^{-1} (P0, P60, P90, P120). Root sampling: Cores to 10 cm; washing, sieving.	Both N and P had positive effects on root growth up to moderate dose. At 10 days after sowing: $P < 90$ kg ha^{-1} increased root number. At later stages: $P = 90, 120$ kg ha^{-1} had higher root number in both genotypes.		(Yang et al., 2021)

Table A.2: Effects of P deficiency and different P application levels on root morphology and root distribution as well as on root biomass. Treatment description: P0 stands for no P fertilizer applied, P(P supply level) stands for the amount of P applied in kg ha^{-1} (e.g. P44: 44 kg P ha^{-1} were applied). A detailed bibliography of the references is included in the main manuscript.

Crop, Site, Soil	**Treatments and sampling**	**Effects on root morphology and distribution**	**Effect on root biomass and root-to-shoot ratio**	**Reference**
Crop: Soybean (two genotypes). Site: China. Soil: Acidic red soil deficient in P	Two P levels: P0 and 160 kg P ha^{-1} (P160). Root sampling: At flowering. Camera and image analysis. Scanned and analyzed with WinRHIZO.	The two parental genotypes, CN4 and XM6, differed significantly in the seven root morph-architecture traits measured. Root length, root surface area, root volume, root width were significantly higher in the treatment with high P. Specific root length and root depth did not show significant differences between the P treatments. The P-efficient genotype established longer and larger root system with preferring distribution in surface layer and kept more active roots and, therefore, had a better growth performance in field than the P-inefficient genotype. Root volume was higher for high P as compared to low P.		(Ao et al., 2010)
Crop: Maize. Site: China. Soil: Silty loam	Eight P application rates: P0, P12.5, P25, P50, P75, P100, P150 and P300 (kg P ha^{-1}). Root sampling: Sampling at flowering.	Root length increased with more P supply until reaching the critical Olsen-P level indicating a plateau at 8 mg kg^{-1}. As soil Olsen-P increased from very low levels, specific root length and root-to-shoot ratio declined substantially at first, and then gradually reached a plateau when Olsen-P exceeded 5 mg kg^{-1}.	In the field experiment, root dry weight also initially increased with increasing soil P supply, peaked when soil Olsen-P was about 2.5 mg kg^{-1}, and then gradually declined to plateau at an Olsen-P level around 10 mg kg^{-1}.	(Deng et al., 2014)

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Crop, Site, Soil	**Treatments and sampling**	**Effects on root morphology and distribution**	**Effect on root biomass and root-to-shoot ratio**	**Reference**
Crop: Oilseed rape. Site: China, 2 yrs. Soil: Yellow-brown soil (Alfisol).	Two P treatments: 90 kg P_2O_5 ha^{-1} (sufficient) and 30 kg P_2O_5 ha^{-1} (deficient). Root sampling: Excavated soil cubes (1000 cm^3).	Root surface area in 0–10 cm soil layer and root length of 2–5 mm root diameter in 0–10 cm soil layer were significantly smaller at deficient P supply. Total root length in 0–10 cm soil layer was less with a deficient P supply. When plants received a deficient P supply, seed yield had significant positive correlations with coarse root length (diameter 2–3 mm), root surface area, and total root length in 0–10 cm soil layer at the flowering stage. The total phosphorus content had significant positive correlations with total root length and root surface area at the flowering stage when plants received a deficient P supply. Plants grown with a deficient P supply had larger total root length ratio and coarse root length ratio in the surface soil (0–10 cm soil layer) and a larger root/shoot ratio at the flowering stage than plants grown with a sufficient P supply. Increased distribution of coarse roots in the surface soil (0–10 cm soil layer) to increase P acquisition at the leaf development and flowering stages.	The root-to-shoot ratio was larger when plants were grown with a deficient P supply than when grown with a sufficient P supply.	(Duan et al., 2020)

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Table A.2 – *Continued from previous page*

Crop, Site, Soil	**Treatments and sampling**	**Effects on root morphology and distribution**	**Effect on root biomass and root-to-shoot ratio**	**Reference**
Crop: Soybean. Site: USA. Soil: Fine-silty.	Three levels of soil P availability (4, 19 and 32 mg kg^{-1}, Mehlich-3 P) and two levels of water (irrigated and non-irrigated). Root sampling: At 78 days after sowing. Root coring (until 36 cm deep). Scanned and analyzed with ROOTEDGE.	P deficiency slowed vegetative development and increased root length density in the surface soil. Increase in root length density with low water availability suggests that water deficit limited P nutrition not by reducing root growth but by decreasing P diffusion in the soil.	—	(Gutierrez-Boem and Thomas, 1998)
Crop: Sugar beet. Site: Germany. Soil: Silty loam	Two P levels: P0 and 160 kg P ha^{-1} (P160). Root sampling: At flowering. Camera and image analysis. Scanned and analyzed with WinRHIZO.	Decreasing total root length under P0 compared with full fertilization, except in the last date. Increasing total root length under P0 compared with no fertilization, except in the second date.	Decreasing of root dry matter in P0 compared with full fertilization, but greater than no fertilization at the beginning and middle stage. Decreasing of root-to-shoot ratio in P0 compared with full fertilization and similar to not fertilized treatment.	(Hadir et al., 2021)
Crop: Common beans (two genotypes). Site: Costa Rica (2 yrs.).	Two sites based on low-phosphorus availability. Phosphorus levels averaged 10 mg kg^{-1} at Site 1 and 8.3 mg kg^{-1} at Site 2 (determined by Mehlich-3 extraction). Root sampling: At flowering. Soil coring (4 cm diameter, 45 cm depth).	Total root length was greater in low P (about 18%) for one genotype but similar (in low and high P) in the other genotype.		(Henry et al., 2010b)

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Table A.2 – *Continued from previous page*

Crop, Site, Soil	**Treatments and sampling**	**Effects on root morphology and distribution**	**Effect on root biomass and root-to-shoot ratio**	**Reference**
Crop: Common beans (two genotypes). Site: Honduras.	Eight sites based on low-phosphorus availability: Low P (3–38 mg P kg^{-1}) and high P (14–252 mg P kg^{-1}), determined by Mehlich-3 extraction. Root sampling: At flowering. Soil coring (4 cm diameter, 60 cm depth).	At the LV4 irrigated site compared to the LV4 drought site: Total root length was not significantly different among genotypes or between single and multilines, but L-88 14 + 43 had on average 80% greater total root length than L-88 14 under drought/high-P, and 44% less total root length than L-88 14 under drought/low-P. In multiline plots, very few roots were found below 45 cm in the high-P treatment whereas root distribution with depth in the low-P treatment was variable.	—	(Henry et al., 2010a)

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Table A.2 – *Continued from previous page*

Crop, Site, Soil	**Treatments and sampling**	**Effects on root morphology and distribution**	**Effect on root biomass and root-to-shoot ratio**	**Reference**
Crop: Soybean (several genotypes). Site: China. Soil: Acid red soil deficient in P.	Two P levels: 0 and 160 kg P ha^{-1} (P160). Cultivated, semi-wild and wild type genotypes. Root sampling: At flowering. Square block of soil (40 cm × 40 cm) with the plant base at the center was dug to reach the end of taproot. Washed, scanned and analyzed using WinRHIZO Pro.	Root architecture was closely related to P efficiency in soybean. The bush cultivated soybean had a shallow root architecture and high P efficiency, the climbing wild soybean had a deep root architecture and low P efficiency, while the root architecture and P efficiency of semi-wild soybean were intermediate between cultivated and wild soybean; Soybean roots became shallower with P addition to the topsoil, indicating that the co-evolutionary relationship between root architecture and P efficiency might be attributed to the long-term effects of topsoil fertilization. Without P addition, most cultivated genotypes had shallow roots and most wild genotypes had deeper roots, and the semi-wild genotypes were mostly intermediate, indicating that the evolutionary pathway of soybean root architecture could be from deep to shallow. However, some semi-wild genotypes became shallow-rooted when P was applied to the topsoil.		(Jing et al., 2004)

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Table A.2 – *Continued from previous page*

Crop, Site, Soil	**Treatments and sampling**	**Effects on root morphology and distribution**	**Effect on root biomass and root-to-shoot ratio**	**Reference**
Crop: Maize. Site: Canada. Soil: Deep clay loam soil.	Three P fertilization treatments: P0, 17.5 (P17), and 35 kg P ha^{-1} (P35). Two tillage treatments. Root sampling: At silking. Root coring, washing, scanning and analysis with WinRHIZO.	In general, higher root mass density, root surface density, and RLD in high P (P1P) but comparing 0P and 0.5P, the values are a bit higher for P0. The root surface density was higher with the 1P than with the 0P and 0.5P application. RLD was 32% (P ¿ 0.05) higher with the 1P than with the 0P and 0.5P applications. P fertilization showed effects on corn roots by having fewer roots, especially primary roots in 0P and 0.5P. The root length density of primary roots was significantly higher in the high P treatment.	The 35 kg P ha^{-1} rate increased the root biomass by 26% and 41% compared to the 0 and 17.5 kg P ha^{-1} rates.	(Li et al., 2017)
Crop: Common beans. Site: Mozambique.	Two P levels: 0 and 100 kg P_2O_5 ha^{-1}. Root sampling: Total root length was measured from excavated root crowns of 3 plants per each of four replications at 28 DAP grown in the field.	Low P treatment fostered the number of adventitious roots. In the topsoil, genotypes with 2 whorls showed greater root length in the treatment with low P. It was otherwise, in the genotype with 3 whorls. In the subsoil the root length was shorter in the low P treatment. Genotypes were also evaluated for root hair length. All genotypes had greater root hair length under low phosphorus availability compared to medium phosphorus availability.		(Miguel et al., 2013)
Crop: Common bean. Site: Mozambique. Soil: Red loam.	The experiment had medium-phosphorus (6 ppm P) and low-phosphorus (19 ppm P). Root sampling: Root coring (30 cm depth), washed, scanned and analyzed in WinRHIZO.	Medium P increased the basal root angle, while low P fostered the length of root hairs.		(Miguel et al., 2015)

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Crop, Site, Soil	**Treatments and sampling**	**Effects on root morphology and distribution**	**Effect on root biomass and root-to-shoot ratio**	**Reference**
Crop: Common bean. Site: Colombia.	Two P levels: 45 kg ha^{-1} and 7.5 kg ha^{-1}. Root sampling: Excavating the plants to reveal as many adventitious and basal roots as possible, and counting the number of adventitious roots emerging from the hypocotyls.		Lower biomass and length of adventitious roots under low P level, but greater number of roots and specific root length.	(Ochoa et al., 2006)
Crop: Buckwheat, castor, peanut, pigeonpea, sorghum, and soybean. Site: Japan (two sites). Soil:	Two P levels: (P0) had received no P fertilizer since 1979, and the other (P90) received 90 kg P ha^{-1}. Root sampling: Through a block dug up along the row at maturity. Root length was measured by the Comair root length scanner.	Root length was higher in high P conditions as compared to P0 (exception: pigeonpea).	—	(Otani and Ae, 1996)
Crop: Maize. Site: Canada (long-term field). Soil: Clay to clay loam.	Three P fertilization treatments: P0, 17.5 (P17), and 35 kg P ha^{-1} (P35). Two tillage treatments. Root sampling: At the 8 to 10 leaf stage. Root coring, washing, scanning, and analysis using WinRHIZO.	P fertilization had significant effects on total root length density and the percentage of fine and coarse roots. The highest total root length density and percentage of fine roots were observed when 35 kg P ha^{-1} was added, while the highest percentage of coarse roots was observed when 17.5 kg P ha^{-1} was added. P fertilization enhanced total root length density, and the percentage of fine roots.	—	(Sheng et al., 2012)

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Table A.2 – *Continued from previous page*

Crop, Site, Soil	**Treatments and sampling**	**Effects on root morphology and distribution**	**Effect on root biomass and root-to-shoot ratio**	**Reference**
Crop: Winter barley. Site: Long-term field. Soil: Loamy.	Two P levels: 0P and 44 kg P ha^{-1} (44P). Root sampling: At 190, 213, 231, 249 and 268 days after sowing. Root coring until 0.3 m soil depth. Root production (gross growth) was measured by the ingrowth core method.	The P fertilization resulted in more roots most of the time, however, these differences were significant only at one date and less pronounced than for the shoot development. Higher root length and root weight increment per shoot increment in 0P compared to treatment with P application in all four sampling dates.	Root-to-shoot ratio was about 60% higher in the 0P treatment over the whole growing period (shoot decrease). 63% and 58% of the total produced roots were already dead at harvest in the 0P and in the treatment with P application.	(Steingrobe et al., 2001)
Crop: Common beans. Site: USA. Soil: Silty loam.	Two P levels: Low-P (10 ppm mean available P–Mehlich-3) and high-P fields (38 ppm mean available P). Root sampling: Flowering. Soil coring (5.1 cm diameter, 40 cm depth), washed, scanned and analyzed with WinRHIZO.	Under P stress, reduced genotypes had 32% greater root length density in the top 40 cm of soil than advanced genotypes, while under high P, no genotypic differences were detectable. Root length density in the top 40 cm was positively correlated with total shoot P under P stress, while no relationship was observed under high P.	—	(Strock et al., 2018)
Crop: Wheat. Site: China, 2 yrs. Soil: Silt fluvo-aquic soil.	Six P levels: 0P, 25P, 50P, 100P, 200P, and 400P (kg P ha^{-1}). Root sampling: At flowering. Soil volumes of 40 × 20 cm to a total depth of 60 cm were dug out.	RLD increased with P-fertilizer rate at first, peaked at P100, and then declined again (P200 and P400).	Root dry weight increased from P0 to P100 and decreased again towards P200 and P400. Root-to-shoot ratio increased from P0 to P400.	(Teng et al., 2013)
Crop: Rice (two hybrid-rice cultivars). Site: China. Soil: Clay-loamy soil.	Four N levels: N0, N60, N120, and N180 (kg N ha^{-1}) and P levels: P0, P60, P90, and P120 (kg ha^{-1}). Root sampling: Soil coring (10 cm deep). Washed and sieved.	Both N and P fertilization had a positive impact on root growth up to moderate dose. At early stage (10 days after sowing), P ¡ 90 kg ha^{-1} favored the number of roots in both genotypes. The number of roots is greater in 90 and 120 kg P ha^{-1} later in the growing period in both genotypes.	—	(Yang et al., 2021)

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Table A.2 – *Continued from previous page*

Crop, Site, Soil	**Treatments and sampling**	**Effects on root morphology and distribution**	**Effect on root biomass and root-to-shoot ratio**	**Reference**
Crop: Maize. Site: China (long-term field). Soil: Loamy and silt (Calcareous alluvial fluvo-aquic).	Two P levels: P0 and 44 kg P ha^{-1} (P44). Root sampling: At jointing, silking and maturity. A soil volume of 50 cm × 20 cm × 60 cm was dug out. Scanned and analyzed with WinRHIZO.	Increasing length in roots in the soil layers 40 to 60 cm at jointing and in the soil layers 30 to 50 cm at silking without P, especially for the fine roots with diameter ¡ 0.6 mm. At maturity, however, the root length of the P100 plants in the whole soil profile was longer than that of the P0 plants, regardless of the root diameter.	Lower root weight without P ($\approx$ 2.5 g per plant) compared with high P application ($\approx$ 5 g per plant) at maturity.	(Zhang et al., 2012)
Crop: Maize. Site: USA. Soil: Silt loam.	Two P treatments: Low P soil averaged 9 ± 0.5 mg P kg^{-1} and high P soil averaged 120 ± 13 mg P kg^{-1}. Recombinant inbred lines (RILs). Root sampling: Plants were harvested at 32 days after planting to collect lateral root hair length (mm).	Genotypes with long root hairs under low P availability had significantly greater plant growth, P uptake, specific P absorption rates and lower metabolic cost-benefit ratios than short-haired genotypes. Root hair length (mm) was greater in low P.		(Zhu et al., 2010)
Crop: common bean. Site: Honduras.	Four P treatment: i) high P and irrigation, ii) low P and irrigation, iii) high P and no irrigation and, iv) low P and no irrigation. Four recombinant inbred lines (2 with shallow basal root and 2 with deep basal roots) and its parent's. Root sampling: At 39 to 41 days after planting Root coring until 0.6m.Scanned and analyzed with WinRHIZO.	In the field, shallow-rooted genotypes surpassed deep-rooted genotypes under combined stress conditions (P0 & rainfed).Total root length density was lower in low P conditions and under rainfed conditions. Genotypes that allocate roots to surface horizons, particularly basal roots, were better adapted to low P environment. Genotypes that allocate root biomass to deep horizons, particularly to the tap root, are better adapted to terminal drought environments.	No significant differences were found between shallow and deep genotype classes for biomass production. Increasing root-to-shoot ratio under low P conditions. Highest root-to-shoot ratio when P and water were limited.	(Zhu et al., 2010)

Table A.3: Effects of K deficiency and different K application levels on root morphology and root distribution as well as on root biomass. Treatment description: K0 stands for no K fertilizer applied, K(K supply level) stands for the amount of K applied in kg ha^{-1} (e.g. K84: 84 kg K ha^{-1} were applied). A detailed bibliography of the references is included in the main manuscript

Crop, Site, Soil	**Treatments and sampling**	**Effects on root morphology and distribution**	**Effect on root biomass and root-to-shoot ratio**	**Reference**
Crop: Soybean. Site: USA, 2 yrs. Soil: silt loam	3 K levels [3]. Root sampling: At V1, V5, R2, R4 and R6 stages. Root coring, washing, scanning and image analysis.	Statistically greater root diameter values in the high-K treatment (2 year mean of 0.274 mm) when compared to low-K (0.252 mm). However, the effect of K treatment on mean root diameter was minor. Calculated root surface area density patterns reflected those of root length density and were not influenced by K treatment. Most K-related differences in above- and below-ground growth and K uptake rates occurred during early reproductive stages when soil surface water and K availability were high.		(Fernández et al., 2009)
Crop: Cotton. Site: USA, 2 yrs. Soil: fine sandy loam	Two K treatments: K0 and K84 (kg K ha^{-1}). Treatments consisted of K rates broadcast on the surface with and without in-row subsoiling, or deep-placed in the subsoil channel. Root sampling: Soil coring.	Root length density decreased from 20 to 80 cm in K0. In the surface 20 cm of soil there were no treatment effects on root density in 1990. In 1991, the greatest root densities (0–20 cm) were observed with broadcast K and no subsoiling.		(Mullins et al., 1994)

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[3] Cumulative K fertilizer applied to individual treatment plots prior to 2002 ranged from 0 to 900 kg K ha^{-1}, creating a broad range of soil K levels. Following 2002, no additional fertilizer K was added to the plots. The ranges in values of soil extractable-K used to assign each fertility treatment were as follows: 54 to 73 mg kg^{-1} in surface (0 to 10 cm soil depth increment) and 46 to 57 mg kg^{-1} in subsurface (10 to 20 cm soil depth increment) for low fertility; 107 to 164 mg kg^{-1} in surface and 60 to 70 mg kg^{-1} in subsurface for medium fertility; and 266 to 316 mg kg^{-1} in surface and 70 to 104 mg kg^{-1} in subsurface for high fertility.

Table A.3 – *Continued from previous page*

Crop, Site, Soil	**Treatments and sampling**	**Effects on root morphology and distribution**	**Effect on root biomass and root-to-shoot ratio**	**Reference**
Crop: Spring Barley. Site: Denmark, 3 yrs. Soil: coarse-textured meltwater sand	Potassium application at rates of 50, 125 and 200 kg K ha^{-1} (K50, K125, K200). Three irrigation factors:[a.] Irrigation at 30 mm deficit of soil water (fully irrigated).[b.] A soil-water deficit of about 50 mm was imposed during early grain filling by shelters. Otherwise as in (a).[c.] Irrigated at a soil-water deficit of 50 mm if reached. Root sampling: 6.5 cm diameter auger to a depth of 50–80 cm in 10 cm layers.	In 1986 root densities were similar at both K (50K and 200K) levels, while in 1987 the root density in the subsoil layers was significantly (P¡0.04) increased by application of 200 kg K ha^{-1} as compared to the density at 50 kg K ha^{-1}.		(Andersen et al., 1992)
Crop: Maize (C1), Sorghum (C2) and Millet (C3). Site: Iran, 3 yrs. Soil: sandy loam	Potassium levels: K0 and K200 (kg ha^{-1}). Irrigation levels: Non-drought stress (S1): leaf relative water content (RWC) ¿ 95%. Drought stress (S2): irrigation under RWC = 60–70%. Root sampling: Auger (height = 100 cm, radius = 15 cm), 24 h after irrigation.	Higher root penetration under K Application. Root length was 111.04 cm under K0 while K200 showed 126.12 cm .K application contributed plants to approach longer root length as well through the condition of drought stress.		(Valadabadi and Farahani, 2009)

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Table A.3 – *Continued from previous page*

Crop, Site, Soil	**Treatments and sampling**	**Effects on root morphology and distribution**	**Effect on root biomass and root-to-shoot ratio**	**Reference**
Crop: Maize. Site: China. Soil: sandy	Two levels of K: 0 and 150 kg of potassium sulfate per ha. Root sampling: Roots for morphology measurement were sampled at seedling, shooting, booting, tasseling and flowering stages. Measured with WinRHIZO.	Under low potassium (–K) treatment, the total root length of 90-21-3 (tolerant to K deficiency) decreased before booting stage, whereas it was increased by 274 cm and 347 cm at shooting and tasseling/flowering stages, respectively. By contrast, the total root length of D937 (sensitive to K deficiency) slightly decreased compared with high potassium (+K) treatment during the whole growing period. Under –K treatment, the total root lengths of 90-21-3 were significantly longer than that of D937 during the later growing period. Notably, an abundant number of lateral roots in 90-21-3 were developed at tasseling and flowering stages under –K treatment, significantly more than those of D937.		(Zhao et al., 2016)
Crop: Sugar beet. Site: Germany. Soil: Silty loam	Three treatments: N0; K182 (182 kg K ha^{-1} including manure); K116 (116 kg K ha^{-1}), all applied for decades. Root sampling: At 38, 66, 93 and 155 days after sowing. Excavated with a shovel (topsoil). Analyzed with WinRHIZO.	Lower total root length in NP_Ca compared with NPKCa+manure and NPKCa, except in the last date. Higher total root length in NP_Ca compared with no fertilization, except in the first sampling date. Lower average root diameter in NP_Ca compared to full fertilization (NPKCa+manure & NPKCa) and no fertilization.	Lower root dry mass (g plant^{-1}) in NP_Ca compared to full fertilization, but similar to no fertilization. Greatest root dry mass in NPKCa+manure. Lower root-to-shoot ratio in NP_Ca compared with full fertilization (NPKCa+manure & NPKCa) and unfertilized.	(Hadir et al., 2021)

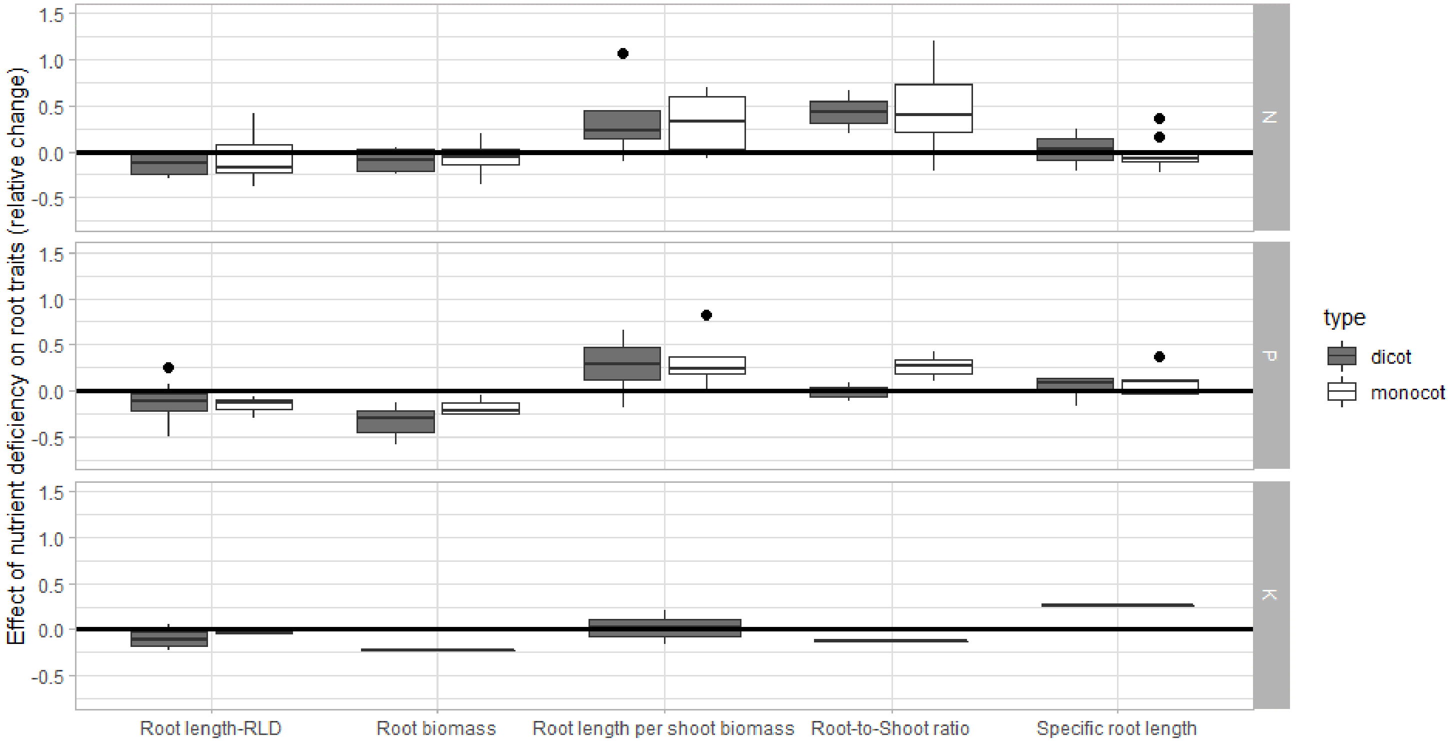

Figure A.1: The relative change of the root traits per type of root (monocot–dicot) under deficiency $\left[(X_0 - X_1)/X_1\right]$, where X_0 is the value in the treatment without any addition of the nutrient and X_1 is the value of the treatment with the nutrient application.

Appendix B

Supplementary material for chapter 3

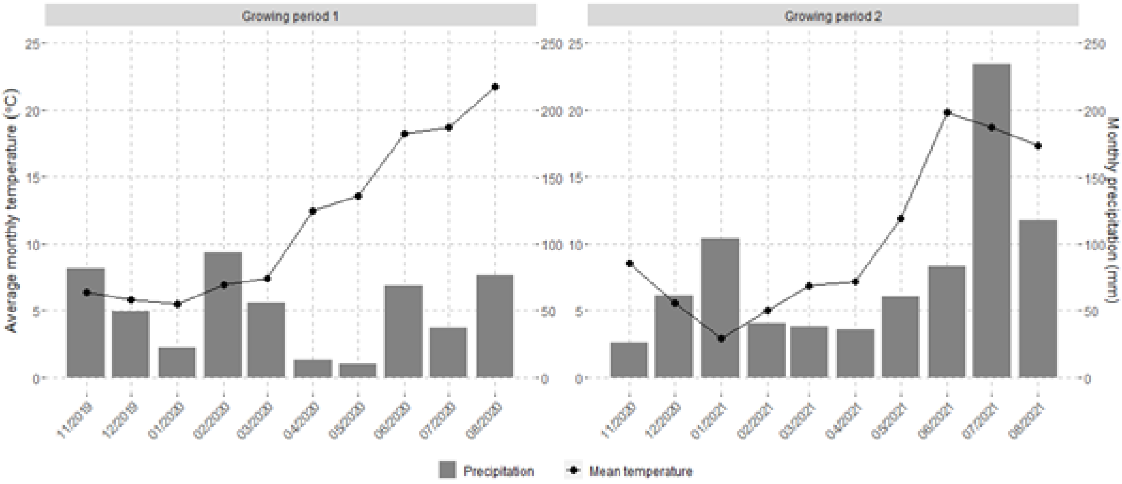

Figure B.1: Monthly rainfall and mean temperature during the winter wheat growing period 1 (2019/20) and growing period 2 (2020/21) at the LTFE Dikopshof (source: interpolated data from the German Weather Service, DWD).

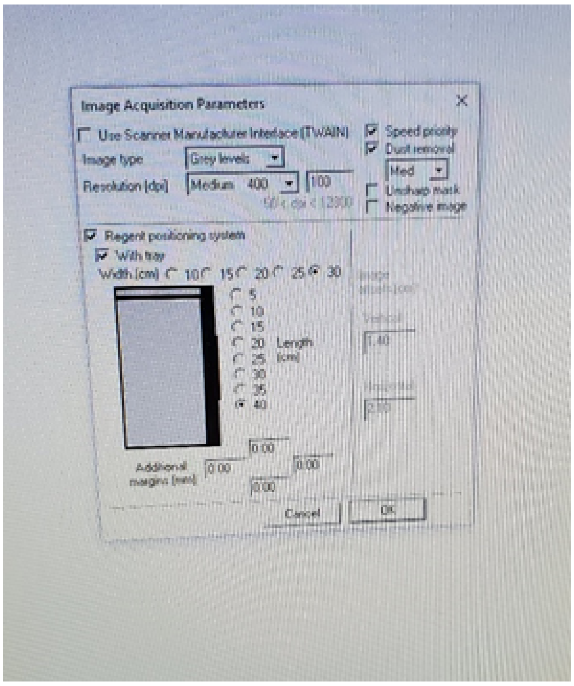

Image Acquisition Parameters

☐ Use Scanner Manufacturer Interface (TWAIN)
Image type: Grey levels
Resolution (dpi): Medium 400 | 100
50 < dpi < 12800
☑ Speed priority
☑ Dust removal: Med
☐ Unsharp mask
☐ Negative image
☑ Regent positioning system
☑ With tray
Width (cm): ○ 10 ○ 15 ○ 20 ○ 25 ● 30
Length (cm): ○ 5 ○ 10 ○ 15 ○ 20 ○ 25 ○ 30 ○ 35 ● 40
Additional margins (mm): 0.00 0.00 0.00 0.00
Vertical: 1.40

Figure B.2: Settings for scanning using WinRHIZO.

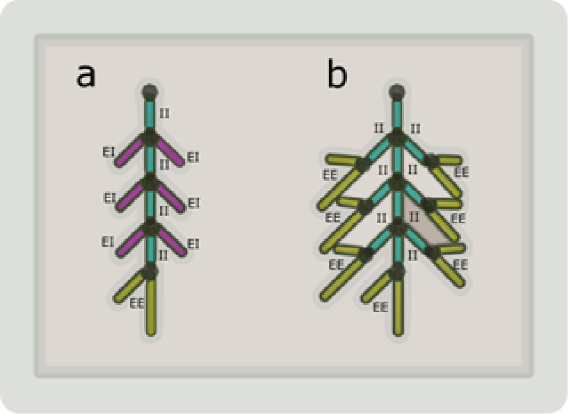

Figure B.3: Type of links in roots: exterior-exterior (EE) in yellow, exterior-interior (EI) in magenta, and interior-interior (II) in blue. According to the predominant type of links the roots could be: a) Herringbone, or b) dichotomous type. Picture source: adapted from Hadir *et al.* (2021) and Fitter (1987).

Table B.1: Mean soil water content (%) ± sd – Growing period 1 (2019/20).

Date	**Depth (cm)**	**NPKCa+m+s**	**NPKCa**	**_PKCa**	**N_KCa**	**NP_Ca**	**NPK_**	**unfertilized**
19-May-20	15	11.6 ± 0.4	13.4 ± 1.1	13.8 ± 1.2	12.3 ± 4.1	13.2 ± 1.3	14.7 ± 1.6	18.3 ± 1.9
	40	15.7 ± 0.8	16.6 ± 2.3	20.9 ± 5.3	15.1 ± 1.0	15.5 ± 2.6	17.6 ± 2.6	25.0 ± 4.7
	65	19.6 ± 3.0	22.2 ± 3.4	24.9 ± 7.5	18.6 ± 1.6	21.6 ± 2.7	25.4 ± 2.4	26.3 ± 5.8
	90	19.8 ± 3.0	21.4 ± 4.6	20.6 ± 3.4	18.1 ± 7.2	18.4 ± 3.6	20.2 ± 1.2	10.7 ± 5.1
26-May-20	15	9.3 ± 1.1	9.3 ± 1.8	10.3 ± 3.8	11.4 ± 0.8	10.2 ± 1.8	12.0 ± 1.9	13.2 ± 2.4
	40	9.6 ± 1.5	12.8 ± 0.5	13.2 ± 2.9	11.6 ± 1.3	12.5 ± 1.1	11.8 ± 1.7	21.3 ± 2.8
	65	18.2 ± 1.8	16.5 ± 3.1	18.3 ± 5.8	17.0 ± 2.0	16.7 ± 2.1	17.7 ± 2.4	24.3 ± 3.4
	90	16.6 ± 2.0	16.3 ± 1.3	13.5 ± 3.4	16.1 ± 2.1	13.9 ± 4.5	14.5 ± 2.3	15.7 ± 3.8
2-Jun-20	15	7.5 ± 1.0	8.3 ± 0.7	10.5 ± 1.6	10.3 ± 1.6	7.3 ± 3.9	9.5 ± 0.7	9.8 ± 2.8
	40	8.9 ± 1.4	9.2 ± 2.9	12.7 ± 5.1	10.8 ± 0.9	11.7 ± 2.7	10.7 ± 0.9	20.1 ± 3.9
	65	11.7 ± 1.2	14.9 ± 2.9	18.6 ± 3.8	14.4 ± 2.0	13.0 ± 3.7	14.1 ± 1.1	19.6 ± 1.1
	90	16.3 ± 3.6	17.1 ± 2.7	19.3 ± 2.7	12.5 ± 1.0	13.0 ± 3.1	13.9 ± 0.7	15.4 ± 6.1
9-Jun-20	15	10.4 ± 0.8	10.7 ± 1.6	11.0 ± 1.6	9.8 ± 0.8	12.1 ± 2.4	12.3 ± 1.4	14.5 ± 3.2
	40	10.4 ± 0.9	11.6 ± 0.7	12.1 ± 3.1	8.8 ± 1.6	10.4 ± 1.5	11.6 ± 0.9	19.5 ± 1.1
	65	12.2 ± 0.8	12.7 ± 0.8	15.8 ± 1.8	11.8 ± 1.2	13.2 ± 1.0	14.0 ± 1.9	22.8 ± 2.6
	90	14.7 ± 0.6	14.8 ± 0.9	14.0 ± 1.5	13.5 ± 3.0	14.4 ± 0.6	11.5 ± 4.1	15.2 ± 4.0
16-Jun-20	15	11.2 ± 1.3	13.1 ± 2.0	13.6 ± 1.8	11.0 ± 1.1	11.9 ± 0.7	12.4 ± 0.8	15.3 ± 2.6
	40	11.5 ± 1.6	11.6 ± 2.1	14.6 ± 2.2	13.3 ± 1.1	11.6 ± 0.6	12.4 ± 0.7	17.4 ± 2.3
	65	13.8 ± 1.8	15.7 ± 3.3	18.8 ± 2.1	15.8 ± 1.0	15.0 ± 1.0	14.2 ± 1.5	18.4 ± 1.8
	90	13.7 ± 0.5	15.5 ± 1.6	18.5 ± 1.9	16.4 ± 2.0	16.3 ± 0.9	15.8 ± 0.5	17.5 ± 2.9
23-Jun-20	15	11.8 ± 0.8	11.4 ± 0.6	13.0 ± 0.6	10.3 ± 0.3	9.9 ± 0.7	10.2 ± 1.1	14.1 ± 2.6
	40	10.5 ± 0.6	11.5 ± 0.8	11.7 ± 1.8	10.6 ± 0.3	10.0 ± 0.9	9.9 ± 1.9	16.5 ± 3.7
	65	11.8 ± 1.5	11.5 ± NA	19.9 ± 3.5	13.8 ± 2.2	13.3 ± 4.1	14.6 ± 1.5	20.1 ± 2.1
	90	14.4 ± 1.4	0.0 ± NA	16.5 ± 6.3	11.2 ± 1.4	15.2 ± 1.0	14.7 ± 3.7	15.8 ± 2.7

Table B.2: Mean soil water content (%) ± sd – Growing period 2 (2020/21).

Date	**Depth (cm)**	**NPKCa+m+s**	**NPKCa**	**_PKCa**	**N_KCa**	**NP_Ca**	**NPK_**	**unfertilized**
5-May-21	0	14.4 ± 2.9	17.1 ± 0.6	17.2 ± 0.5	18.6 ± 1.2	16.6 ± 1.2	18.6 ± 1.7	16.0 ± 0.7
	30	22.7 ± 4.6	17.6 ± 3.6	25.9 ± 7.4	25.6 ± 4.4	23.2 ± 8.5	24.0 ± 6.6	24.6 ± 9.7
	60	24.6 ± 3.0	22.9 ± 6.8	30.2 ± 3.6	29.2 ± 7.5	29.4 ± 8.8	31.9 ± 6.0	35.0 ± 1.5
	90	20.1 ± 2.1	17.7 ± 6.5	14.9 ± 4.4	9.6 ± 1.8	29.8 ± NA	15.6 ± 3.5	13.7 ± NA
19-May-21	0	30.6 ± 4.5	32.5 ± 0.8	30.2 ± 2.5	29.7 ± 2.2	28.4 ± 1.4	30.8 ± 0.5	28.7 ± 1.6
	30	17.2 ± 2.3	20.7 ± 5.0	16.9 ± 3.0	19.0 ± 0.7	14.4 ± 6.2	15.6 ± 0.4	21.0 ± 2.2
	60	23.2 ± 3.6	23.9 ± 3.1	22.6 ± 2.0	22.3 ± 3.1	19.4 ± 1.7	22.1 ± 3.6	25.3 ± 4.0
	90	21.6 ± 8.0	7.6 ± 2.3	10.8 ± NA	12.4 ± 6.4	9.8 ± 0.7	17.6 ± 3.6	15.6 ± 2.6
2-Jun-21	0	15.5 ± 4.2	13.8 ± 2.2	18.6 ± 1.2	15.7 ± 0.3	18.0 ± 0.9	17.3 ± 2.4	17.4 ± 0.3
	30	19.3 ± 1.0	16.3 ± 3.6	25.0 ± 5.5	19.8 ± 2.7	15.9 ± 2.5	12.3 ± 2.1	20.0 ± 4.1
	60	20.2 ± 2.3	22.1 ± 1.2	23.1 ± 4.8	24.0 ± 2.7	20.7 ± 0.6	22.0 ± 3.4	22.7 ± 6.4
	90	21.2 ± 5.4	20.0 ± 9.7	14.3 ± 2.7	10.1 ± 4.1	16.5 ± 3.5	14.8 ± 2.6	13.8 ± 0.7
16-Jun-21	0	6.1 ± 1.0	9.6 ± 1.7	12.8 ± 2.1	12.6 ± 0.8	9.7 ± 1.0	10.9 ± 2.6	12.7 ± 2.4
	30	6.9 ± 0.9	16.4 ± 1.2	14.1 ± 0.6	16.4 ± 2.3	15.0 ± 1.5	14.7 ± 3.7	20.2 ± 4.6
	60	11.8 ± 1.0	22.8 ± 2.1	22.2 ± 0.7	21.5 ± 1.4	23.3 ± 5.2	18.1 ± 1.4	23.9 ± 5.9
	90	16.1 ± 0.0	8.5 ± 3.4	16.8 ± 1.2	20.4 ± 0.7	6.6 ± NA	8.0 ± 1.2	10.1 ± 2.0

Table B.3: Topsoil nutrient content at the first soil–root sampling campaign during 2019/20 (BBCH 23).

Treatment	**Layer**	**NPKCa+m+s**	**NPKCa**	**_PKCa**	**N_Ca**	**NP_Ca**	**NPK_**	**unfertilized**
pH	0–30 cm	6.6	6.8	6.8	6.8	6.8	6.5	5.8
Nmin (kg ha^{-1})	0–30 cm	13.8	6.8	7.0	4.7	5.6	3.9	4.8
Kcal (mg kg^{-1})	0–30 cm	354	164	161	111	38	62	48
Pcal (mg kg^{-1})	0–30 cm	174	119	129	25	110	114	30

Table B.4: Topsoil and subsoil nutrient concentrations at the second soil–root sampling campaign during winter wheat booting in 2020 (BBCH 43).

Treatment	**Layer**	**NPKCa+m+s**	**NPKCa**	**_PKCa**	**N_KCa**	**NP_Ca**	**NPK_**	**unfertilized**
pH	0–30	6.6	6.7	6.8	6.8	6.1	5.5	5.9
	30–50	6.7	6.7	7.0	6.8	6.3	6.0	6.1
	50–100	7.0	7.0	7.0	6.9	6.6	6.3	6.2
C (%)	0–30	1.3	0.8	0.8	0.8	0.6	0.8	0.7
	30–50	0.8	0.6	0.5	0.8	0.3	0.6	0.5
	50–100	0.3	0.4	0.3	0.7	0.3	0.4	0.3
N (%)	0–30	0.1	0.1	0.1	0.1	0.1	0.1	0.1
	30–50	0.1	0.1	0.1	0.1	0.0	0.1	0.1
	50–100	0.0	0.0	0.0	0.1	0.0	0.1	0.0
Nmin (kg ha^{-1})	0–30	26.0	13.0	5.1	11.8	18.4	12.1	4.6
	30–50	4.9	1.8	1.4	2.9	3.8	3.0	1.5
	50–100	10.0	2.4	2.0	2.0	3.9	8.3	2.4
Kcal (mg kg^{-1})	0–30	417	112	206	90	61	79	41
	30–50	351	84	97	47	52	58	51
	50–100	144	56	40	48	42	42	43
Pcal (mg kg^{-1})	0–30	201	117	61	43	116	63	19
	30–50	152	69	34	9	85	21	0
	50–100	25	0	0	2	0	0	0

Table B.5: Topsoil and subsoil nutrient concentrations at the first soil–root sampling campaign at flowering 2020/21 (BBCH 69).

Treatment	**Layer**	**NPKCa+m+s**	**NPKCa**	**_PKCa**	**N_Ca**	**NP_Ca**	**NPK_**	**unfertilized**
pH	0–30	6.6	6.1	6.7	6.1	6.1	5.6	6.1
	30–60	6.6	6.2	6.7	5.9	6.2	5.5	6.0
	60–90	7.1	6.9	6.9	6.7	6.6	6.3	6.2
C (%)	0–30	1.1	0.8	0.7	0.8	0.7	0.7	0.7
	30–60	0.7	0.6	0.5	0.7	0.6	0.7	0.5
	60–90	0.3	0.3	0.3	0.3	0.3	0.4	0.3
N (%)	0–30	0.1	0.1	0.1	0.1	0.1	0.1	0.1
	30–60	0.1	0.1	0.1	0.1	0.1	0.1	0.1
	60–90	0.1	0.1	0.1	0.1	0.1	0.1	0.1
Nmin (kg ha^{-1})	0–30	6.7	3.6	2.6	3.9	2.3	6.5	2.9
	30–60	1.2	3.5	1.0	3.2	0.8	2.6	2.3
	60–90	0.7	1.9	0.3	1.5	0.3	1.5	1.8
NO_3–N (mg kg^{-1})	0–30	5.8	2.4	1.9	1.3	0.9	2.0	0.8
	30–60	1.2	1.8	0.7	0.8	0.3	0.4	0.5
	60–90	0.3	0.4	0.1	0.0	0.0	0.0	0.0
NH_4–N (mg kg^{-1})	0–30	1.0	1.2	0.7	2.6	1.4	4.5	2.0
	30–60	0.1	1.7	0.3	2.4	0.5	2.2	1.9
	60–90	0.4	1.6	0.2	1.5	0.3	1.5	1.8
Kcal (mg kg^{-1})	0–30	283	114	126	110	31	125	38
	30–60	202	79	82	89	29	75	39
	60–90	72	57	44	41	46	47	42
Pcal (mg kg^{-1})	0–30	205	75	76	15	74	46	31
	30–60	140	46	36	12	46	44	22
	60–90	11	11	9	4	8	12	10

Table B.6: Roots traits (BBCH 23) - Period 1 (2019-2020)

Trait	Layer	NPKCa+m+s	NPKCa	_PKCa	N_KCa	NP_Ca	NPK_	Unfertilized
Root Biomass (ton ha^{-1})	0–10	0.11 ± 0.01	0.07 ± 0.06	0.08 ± 0.05	0.03 ± 0.01	0.04 ± 0.05	0.08 ± 0.04	0.02 ± 0.02
	10–20	0.07 ± 0.05	0.06 ± 0.02	0.06 ± 0.04	0.03 ± 0.02	0.04 ± 0.02	0.06 ± 0.02	0.02 ± 0.01
	20–30	0.05 ± 0.03	0.05 ± 0.01	0.03 ± 0.02	0.01 ± 0.01	0.02 ± 0.01	0.03 ± 0.02	0.01 ± 0.02
	30–40	0.02 ± 0.02	0.03 ± 0.03	0.01 ± 0.01	0.01 ± 0.01	0.01 ± 0.01	0.02 ± 0.01	0.00 ± 0.01
	40–50	0.02 ± 0.01	0.01 ± 0.01	0.00 ± 0.01	0.01 ± 0.01	0.01 ± 0.02	0.01 ± 0.01	0.00 ± 0.00
	50–60	0.00 ± 0.00	0.00 ± 0.01	0.00 ± 0.00	0.00 ± 0.01	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
	60–70	0.00 ± 0.00	0.01 ± 0.02	0.00 ± 0.00	0.01 ± 0.01	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
	Topsoil (0–30 cm)	0.23 ± 0.07	0.17 ± 0.07	0.17 ± 0.08	0.06 ± 0.04	0.10 ± 0.05	0.17 ± 0.07	0.04 ± 0.07
	Subsoil (30–70 cm)	0.04 ± 0.03	0.04 ± 0.03	0.02 ± 0.02	0.02 ± 0.03	0.03 ± 0.03	0.02 ± 0.02	0.00 ± 0.02
	Total (0–70 cm)	0.27 ± 0.08	0.21 ± 0.08	0.18 ± 0.08	0.09 ± 0.06	0.12 ± 0.04	0.19 ± 0.08	0.05 ± 0.04
Total Root Length (cm)	0–10	741.4 ± 169.4	748.2 ± 201.2	603.4 ± 495.7	197.4 ± 192.9	324.2 ± 489.7	1015.4 ± 341.0	158.3 ± 165.5
	10–20	490.3 ± 228.8	760.5 ± 113.5	540.6 ± 289.3	188.0 ± 209.9	251.8 ± 186.6	792.5 ± 189.1	292.4 ± 157.3
	20–30	526.0 ± 182.0	361.3 ± 148.8	185.1 ± 96.4	27.6 ± 22.4	148.9 ± 97.6	268.9 ± 113.0	105.6 ± 54.8
	30–40	137.9 ± 99.2	85.0 ± 52.0	41.3 ± 16.8	19.4 ± 14.1	55.9 ± 27.4	97.3 ± 57.0	52.0 ± 26.2
	40–50	99.1 ± 72.2	37.4 ± 46.9	19.3 ± 5.6	14.7 ± 9.2	29.7 ± 10.8	50.8 ± 44.2	55.2 ± 50.5
	50–60	27.3 ± 10.2	20.7 ± 17.8	18.4 ± 15.2	12.2 ± 8.8	11.1 ± 6.3	16.7 ± 12.1	83.5 ± 47.6
	60–70	35.9 ± 5.7	23.9 ± 38.9	10.8 ± 13.8	7.5 ± 3.9	17.8 ± 10.6	21.2 ± 2.7	19.6 ± 7.7
	Topsoil (0–30 cm)	1757.8 ± 346.8	1870.0 ± 260.4	1329.1 ± 862.7	413.0 ± 407.3	724.9 ± 572.2	2076.8 ± 631.9	556.2 ± 214.1
	Subsoil (30–70 cm)	300.2 ± 117.6	167.0 ± 81.1	89.8 ± 25.1	53.9 ± 21.4	114.5 ± 28.2	186.1 ± 75.4	210.3 ± 99.1
	Total (0–70 cm)	2058.0 ± 457.5	2037.0 ± 205.9	1418.8 ± 855.8	465.9 ± 389.3	839.4 ± 545.2	2262.8 ± 602.1	766.6 ± 224.9
RLD (cm cm^{-3})	0–10	1.17 ± 0.27	1.18 ± 0.32	0.95 ± 0.78	0.31 ± 0.31	0.51 ± 0.77	1.60 ± 0.53	0.25 ± 0.26
	10–20	0.77 ± 0.36	1.20 ± 0.18	0.85 ± 0.45	0.30 ± 0.33	0.40 ± 0.29	1.25 ± 0.30	0.46 ± 0.25
	20–30	0.83 ± 0.29	0.57 ± 0.23	0.29 ± 0.15	0.05 ± 0.03	0.23 ± 0.16	0.43 ± 0.18	0.17 ± 0.09
	30–40	0.22 ± 0.16	0.14 ± 0.08	0.07 ± 0.03	0.03 ± 0.02	0.09 ± 0.04	0.15 ± 0.09	0.08 ± 0.04
	40–50	0.16 ± 0.11	0.06 ± 0.08	0.03 ± 0.01	0.02 ± 0.02	0.05 ± 0.02	0.08 ± 0.07	0.09 ± 0.08
	50–60	0.04 ± 0.02	0.03 ± 0.03	0.03 ± 0.02	0.02 ± 0.01	0.02 ± 0.01	0.03 ± 0.02	0.13 ± 0.07
	60–70	0.06 ± 0.01	0.04 ± 0.06	0.02 ± 0.02	0.01 ± 0.01	0.03 ± 0.02	0.04 ± 0.01	0.03 ± 0.01
	Topsoil (0–30 cm)	0.92 ± 0.181	0.98 ± 0.137	0.70 ± 0.452	0.22 ± 0.213	0.38 ± 0.301	1.09 ± 0.331	0.29 ± 0.113
	Subsoil (30–70 cm)	0.12 ± 0.047	0.07 ± 0.033	0.04 ± 0.011	0.02 ± 0.008	0.05 ± 0.012	0.07 ± 0.029	0.08 ± 0.040
	Total (0–70 cm)	0.46 ± 0.10	0.46 ± 0.05	0.32 ± 0.19	0.11 ± 0.09	0.19 ± 0.12	0.51 ± 0.13	0.17 ± 0.05
RMD (mg cm^{-3})	0–10	0.11 ± 0.01	0.07 ± 0.05	0.08 ± 0.05	0.02 ± 0.01	0.03 ± 0.05	0.08 ± 0.04	0.02 ± 0.02
	10–20	0.07 ± 0.05	0.06 ± 0.02	0.06 ± 0.04	0.03 ± 0.02	0.04 ± 0.02	0.05 ± 0.02	0.01 ± 0.00
	20–30	0.05 ± 0.03	0.05 ± 0.01	0.03 ± 0.02	0.01 ± 0.01	0.02 ± 0.00	0.03 ± 0.02	0.01 ± 0.01
	30–40	0.02 ± 0.02	0.03 ± 0.03	0.01 ± 0.01	0.01 ± 0.01	0.01 ± 0.01	0.01 ± 0.01	0.00 ± 0.00
	40–50	0.01 ± 0.01	0.01 ± 0.01	0.00 ± 0.00	0.01 ± 0.00	0.01 ± 0.02	0.01 ± 0.01	0.00 ± 0.00
	50–60	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00

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Trait	Layer	NPKCa+m+s	NPKCa	_PKCa	N_KCa	NP_Ca	NPK_	Unfertilized
	60–70	0.00 ± 0.00	0.01 ± 0.01	0.00 ± 0.00	0.01 ± 0.01	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
	Topsoil (0–30 cm)	0.08 ± 0.02	0.06 ± 0.02	0.06 ± 0.03	0.02 ± 0.01	0.03 ± 0.02	0.06 ± 0.02	0.01 ± 0.01
	Subsoil (30–70 cm)	0.01 ± 0.01	0.01 ± 0.01	0.01 ± 0.00	0.01 ± 0.00	0.01 ± 0.01	0.01 ± 0.00	0.00 ± 0.00
	Total (0–70 cm)	0.04 ± 0.01	0.03 ± 0.01	0.03 ± 0.01	0.01 ± 0.01	0.02 ± 0.01	0.03 ± 0.01	0.00 ± 0.00
Average Diameter (mm)	0–10	0.26 ± 0.08	0.23 ± 0.06	0.25 ± 0.09	0.12 ± 0.01	0.16 ± 0.06	0.23 ± 0.02	0.17 ± 0.06
	10–20	0.24 ± 0.05	0.23 ± 0.03	0.28 ± 0.14	0.17 ± 0.06	0.18 ± 0.07	0.25 ± 0.03	0.17 ± 0.04
	20–30	0.28 ± 0.04	0.40 ± 0.09	0.25 ± 0.13	0.13 ± 0.03	0.16 ± 0.04	0.30 ± 0.05	0.22 ± 0.05
	30–40	0.36 ± 0.06	0.29 ± 0.16	0.22 ± 0.10	0.15 ± 0.05	0.21 ± 0.12	0.27 ± 0.06	0.18 ± 0.10
	40–50	0.37 ± 0.05	0.28 ± 0.10	0.15 ± 0.05	0.15 ± 0.03	0.21 ± 0.07	0.33 ± 0.10	0.28 ± 0.17
	50–60	0.15 ± 0.04	0.27 ± 0.15	0.23 ± 0.07	0.16 ± 0.01	0.18 ± 0.03	0.17 ± 0.11	0.15 ± 0.03
	60–70	0.13 ± 0.01	0.17 ± 0.03	0.14 ± 0.02	0.13 ± 0.02	0.15 ± 0.04	0.11 ± 0.01	0.15 ± 0.03
	Topsoil (0–30 cm)	0.26 ± 0.04	0.29 ± 0.025	0.26 ± 0.08	0.14 ± 0.01	0.16 ± 0.04	0.26 ± 0.02	0.19 ± 0.02
	Subsoil (30–70 cm)	0.25 ± 0.07	0.25 ± 0.045	0.18 ± 0.04	0.15 ± 0.00	0.19 ± 0.04	0.22 ± 0.05	0.19 ± 0.06
	Total (0–70 cm)	0.26 ± 0.03	0.27 ± 0.03	0.22 ± 0.03	0.14 ± 0.00	0.18 ± 0.02	0.24 ± 0.03	0.19 ± 0.03

Table B.7: Roots traits (BBCH 43) - Period 1 (2019-2020)

Trait	Layer	NPKCa+m+s	NPKCa	_PKCa	N_KCa	NP_Ca	NPK_	Unfertilized
Root Biomass (ton ha^{-1})	0–10	0.17 ± 0.10	0.15 ± 0.09	0.08 ± 0.02	0.13 ± 0.09	0.23 ± 0.14	0.18 ± 0.09	0.07 ± 0.03
	10–20	0.20 ± 0.05	0.09 ± 0.01	0.07 ± 0.03	0.20 ± 0.03	0.10 ± 0.02	0.06 ± 0.02	0.05 ± 0.03
	20–30	0.16 ± 0.07	0.13 ± 0.05	0.09 ± 0.04	0.22 ± 0.06	0.13 ± 0.06	0.14 ± 0.11	0.09 ± 0.03
	30–40	0.11 ± 0.07	0.08 ± 0.03	0.03 ± 0.02	0.11 ± 0.05	0.05 ± 0.02	0.10 ± 0.05	0.07 ± 0.02
	40–50	0.09 ± 0.01	0.09 ± 0.05	0.05 ± 0.01	0.11 ± 0.06	0.06 ± 0.02	0.07 ± 0.03	0.04 ± 0.01
	50–60	0.09 ± 0.03	0.10 ± 0.04	0.06 ± 0.03	0.11 ± 0.02	0.08 ± 0.02	0.07 ± 0.03	0.04 ± 0.01
	60–70	0.10 ± 0.02	0.09 ± 0.03	0.05 ± 0.03	0.13 ± 0.06	0.07 ± 0.02	0.06 ± 0.04	0.05 ± 0.03
	70–80	0.05 ± 0.06	0.08 ± 0.04	0.03 ± 0.01	0.10 ± 0.07	0.07 ± 0.02	0.06 ± 0.03	0.05 ± 0.03
	80–90	0.06 ± 0.05	0.05 ± 0.03	0.03 ± 0.03	0.07 ± 0.02	0.05 ± 0.02	0.04 ± 0.02	0.03 ± 0.01
	90–100	0.06 ± 0.04	0.08 ± 0.04	0.02 ± 0.01	0.04 ± 0.03	0.03 ± 0.00	0.01 ± 0.01	0.01 ± 0.01
	Topsoil (0–30cm)	0.53 ± 0.12	0.37 ± 0.06	0.25 ± 0.05	0.55 ± 0.15	0.46 ± 0.11	0.38 ± 0.16	0.22 ± 0.03
	Subsoil (0–100cm)	0.55 ± 0.10	0.57 ± 0.14	0.29 ± 0.06	0.68 ± 0.25	0.43 ± 0.11	0.40 ± 0.14	0.28 ± 0.08
	Total (0–100cm)	1.08 ± 0.16	0.93 ± 0.15	0.54 ± 0.10	1.23 ± 0.40	0.89 ± 0.10	0.79 ± 0.14	0.50 ± 0.05
Total Root Length (cm)	0–10	1884 ± 723	1402 ± 693	1263 ± 98	1352 ± 1063	1531 ± 883	1611 ± 383	714 ± 449
	10–20	2448 ± 932	1314 ± 310	1794 ± 239	2123 ± 322	1625 ± 35	1208 ± 362	987 ± 87
	20–30	2751 ± 766	1662 ± 778	1774 ± 1262	2947 ± 1520	2706 ± 719	1602 ± 350	1778 ± 820
	30–40	1358 ± 987	667 ± 101	476 ± 76	1434 ± 805	504 ± 136	1173 ± 304	1056 ± 196
	40–50	968 ± 236	696 ± 290	535 ± 206	1160 ± 469	704 ± 239	1150 ± 292	747 ± 66
	50–60	1032 ± 285	1128 ± 382	755 ± 328	1210 ± 402	1088 ± 286	1022 ± 320	580 ± 124
	60–70	1079 ± 549	1036 ± 200	830 ± 329	1344 ± 474	1182 ± 426	945 ± 379	777 ± 367
	70–80	563 ± 620	1000 ± 211	672 ± 143	1019 ± 447	1239 ± 148	1064 ± 624	749 ± 310
	80–90	812 ± 518	909 ± 249	681 ± 195	974 ± 270	1046 ± 166	622 ± 372	379 ± 100
	90–100	750 ± 638	355 ± 341	169 ± 88	234 ± 140	374 ± 110	102 ± 83	107 ± 110
	Topsoil (0–30cm)	7084 ± 1593	4378 ± 284	4831 ± 1465	6423 ± 2401	5861 ± 709	4421 ± 362	3480 ± 1089
	Subsoil (30–100cm)	6563 ± 677	5790 ± 1086	4117 ± 720	7375 ± 2266	6136 ± 735	6078 ± 1811	4395 ± 881
	Total (0–100cm)	13646 ± 1885	10168 ± 1114	8949 ± 2173	13798 ± 4484	11998 ± 834	10499 ± 1916	7875 ± 1423
RLD (cm cm^{-3})	0–10	2.96 ± 1.14	2.20 ± 1.09	1.53 ± 0.15	2.12 ± 1.67	2.41 ± 1.39	2.53 ± 0.60	1.12 ± 0.71
	10–20	3.85 ± 1.47	2.06 ± 0.49	2.82 ± 0.37	3.34 ± 0.51	2.55 ± 0.06	1.90 ± 0.57	1.55 ± 0.14
	20–30	4.33 ± 1.20	2.61 ± 1.22	2.79 ± 1.98	4.63 ± 2.39	4.25 ± 1.13	2.52 ± 0.55	2.80 ± 1.29
	30–40	2.13 ± 1.55	1.05 ± 0.16	0.75 ± 0.12	2.25 ± 1.27	0.79 ± 0.21	1.84 ± 0.48	1.66 ± 0.31
	40–50	1.52 ± 0.37	1.09 ± 0.46	0.84 ± 0.32	1.82 ± 0.74	1.11 ± 0.37	1.81 ± 0.46	1.17 ± 0.10
	50–60	1.62 ± 0.45	1.77 ± 0.60	1.19 ± 0.52	1.90 ± 0.63	1.71 ± 0.45	1.61 ± 0.50	0.97 ± 0.20
	60–70	1.70 ± 0.86	1.63 ± 0.31	1.31 ± 0.52	2.11 ± 0.74	1.86 ± 0.67	1.49 ± 0.60	1.22 ± 0.58
	70–80	0.89 ± 0.97	1.57 ± 0.33	1.06 ± 0.22	1.60 ± 0.70	1.95 ± 0.23	1.67 ± 0.98	1.18 ± 0.49
	80–90	1.28 ± 0.81	1.43 ± 0.39	1.07 ± 0.31	1.53 ± 0.42	1.64 ± 0.26	0.98 ± 0.58	0.60 ± 0.16
	90–100	1.18 ± 1.00	0.56 ± 0.54	0.26 ± 0.14	0.37 ± 0.22	0.59 ± 0.17	0.16 ± 0.13	0.17 ± 0.17
	Topsoil (0–30cm)	3.71 ± 0.88	2.29 ± 0.15	2.53 ± 0.77	3.37 ± 1.26	3.07 ± 0.37	2.32 ± 0.19	1.82 ± 0.57

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Trait	Layer	NPKCa+m+s	NPKCa	_PKCa	N_KCa	NP_Ca	NPK_	Unfertilized
	Subsoil (30–100cm)	1.47 ± 0.15	1.30 ± 0.24	0.92 ± 0.16	1.66 ± 0.51	1.38 ± 0.17	1.36 ± 0.41	0.99 ± 0.20
	Total (0–100cm)	2.15 ± 0.30	1.60 ± 0.18	1.41 ± 0.34	2.17 ± 0.70	1.88 ± 0.13	1.65 ± 0.30	1.24 ± 0.22
RMD (mg cm^{-3})	0–10	0.17 ± 0.10	0.15 ± 0.09	0.08 ± 0.02	0.13 ± 0.09	0.23 ± 0.14	0.18 ± 0.09	0.06 ± 0.03
	10–20	0.20 ± 0.05	0.09 ± 0.01	0.07 ± 0.03	0.20 ± 0.03	0.10 ± 0.02	0.06 ± 0.02	0.07 ± 0.03
	20–30	0.16 ± 0.07	0.13 ± 0.05	0.09 ± 0.04	0.22 ± 0.06	0.13 ± 0.06	0.14 ± 0.11	0.09 ± 0.03
	30–40	0.11 ± 0.07	0.08 ± 0.03	0.03 ± 0.02	0.11 ± 0.05	0.05 ± 0.02	0.10 ± 0.05	0.07 ± 0.02
	40–50	0.09 ± 0.01	0.09 ± 0.04	0.05 ± 0.01	0.11 ± 0.06	0.06 ± 0.02	0.07 ± 0.03	0.04 ± 0.01
	50–60	0.09 ± 0.03	0.10 ± 0.04	0.06 ± 0.03	0.11 ± 0.02	0.08 ± 0.02	0.07 ± 0.03	0.04 ± 0.01
	60–70	0.10 ± 0.02	0.09 ± 0.03	0.05 ± 0.03	0.13 ± 0.06	0.07 ± 0.02	0.06 ± 0.04	0.05 ± 0.03
	70–80	0.05 ± 0.06	0.08 ± 0.04	0.03 ± 0.01	0.10 ± 0.07	0.07 ± 0.02	0.06 ± 0.03	0.05 ± 0.03
	80–90	0.06 ± 0.05	0.05 ± 0.03	0.03 ± 0.03	0.07 ± 0.02	0.05 ± 0.02	0.04 ± 0.02	0.03 ± 0.01
	90–100	0.06 ± 0.04	0.08 ± 0.04	0.02 ± 0.01	0.04 ± 0.03	0.03 ± 0.00	0.01 ± 0.01	0.01 ± 0.01
	Topsoil (0–30cm)	0.18 ± 0.04	0.12 ± 0.02	0.08 ± 0.02	0.18 ± 0.05	0.15 ± 0.04	0.13 ± 0.05	0.07 ± 0.01
	Subsoil (30–100cm)	0.08 ± 0.01	0.08 ± 0.02	0.04 ± 0.01	0.10 ± 0.04	0.08 ± 0.02	0.08 ± 0.03	0.06 ± 0.03
	Total (0–100cm)	0.12 ± 0.02	0.10 ± 0.01	0.06 ± 0.01	0.12 ± 0.02	0.12 ± 0.01	0.10 ± 0.02	0.07 ± 0.01
Average Diameter (mm)	0–10	0.24 ± 0.07	0.20 ± 0.01	0.18 ± 0.01	0.19 ± 0.02	0.23 ± 0.03	0.22 ± 0.04	0.26 ± 0.11
	10–20	0.21 ± 0.01	0.19 ± 0.01	0.19 ± 0.01	0.20 ± 0.02	0.20 ± 0.01	0.19 ± 0.00	0.21 ± 0.03
	20–30	0.19 ± 0.02	0.19 ± 0.01	0.20 ± 0.01	0.20 ± 0.01	0.21 ± 0.01	0.19 ± 0.01	0.19 ± 0.02
	30–40	0.20 ± 0.03	0.25 ± 0.02	0.26 ± 0.01	0.23 ± 0.03	0.23 ± 0.03	0.21 ± 0.01	0.21 ± 0.02
	40–50	0.21 ± 0.01	0.23 ± 0.01	0.25 ± 0.01	0.20 ± 0.01	0.23 ± 0.02	0.19 ± 0.01	0.20 ± 0.01
	50–60	0.22 ± 0.03	0.22 ± 0.02	0.22 ± 0.02	0.22 ± 0.02	0.22 ± 0.02	0.20 ± 0.02	0.20 ± 0.01
	60–70	0.21 ± 0.02	0.23 ± 0.01	0.22 ± 0.02	0.21 ± 0.02	0.19 ± 0.01	0.21 ± 0.02	0.20 ± 0.02
	70–80	0.18 ± 0.05	0.22 ± 0.01	0.24 ± 0.02	0.22 ± 0.05	0.21 ± 0.01	0.20 ± 0.02	0.20 ± 0.01
	80–90	0.22 ± 0.06	0.21 ± 0.03	0.23 ± 0.03	0.23 ± 0.03	0.24 ± 0.03	0.20 ± 0.02	0.22 ± 0.03
	90–100	0.23 ± 0.01	0.21 ± 0.01	0.23 ± 0.02	0.24 ± 0.01	0.24 ± 0.02	0.22 ± 0.00	0.22 ± 0.04
	Topsoil (0–30cm)	0.21 ± 0.03	0.19 ± 0.01	0.19 ± 0.01	0.20 ± 0.01	0.21 ± 0.01	0.20 ± 0.01	0.21 ± 0.01
	Subsoil (30–100cm)	0.21 ± 0.01	0.22 ± 0.01	0.24 ± 0.01	0.22 ± 0.01	0.22 ± 0.01	0.20 ± 0.00	0.20 ± 0.01
	Total (0–100cm)	0.21 ± 0.01	0.22 ± 0.01	0.22 ± 0.01	0.21 ± 0.01	0.22 ± 0.01	0.20 ± 0.00	0.20 ± 0.01

Table B.8: Roots traits (BBCH 69) - Period 2 (2020-2021)

Trait	Layer	NPKCa+m+s	NPKCa	_PKCa	N_KCa	NP_Ca	NPK_	Unfertilized
Root Biomass (ton ha^{-1})	0–10	1.56 ± 0.52	1.74 ± 1.33	0.41 ± 0.17	1.34 ± 0.53	2.00 ± 0.23	1.88 ± 0.09	0.05 ± 0.03
	10–20	0.20 ± 0.04	0.14 ± 0.03	0.08 ± 0.03	0.18 ± 0.04	0.19 ± 0.10	0.23 ± 0.05	0.10 ± 0.01
	20–30	0.28 ± 0.03	0.12 ± 0.01	0.07 ± 0.03	0.20 ± 0.03	0.26 ± 0.09	0.23 ± 0.06	0.10 ± 0.04
	30–40	0.13 ± 0.04	0.07 ± 0.00	0.02 ± 0.02	0.10 ± 0.03	0.13 ± 0.06	0.14 ± 0.11	0.09 ± 0.03
	40–50	0.12 ± 0.03	0.07 ± 0.00	0.04 ± 0.01	0.08 ± 0.03	0.09 ± 0.01	0.08 ± 0.02	0.03 ± 0.01
	50–60	0.13 ± 0.06	0.09 ± 0.03	0.05 ± 0.02	0.09 ± 0.03	0.11 ± 0.02	0.07 ± 0.02	0.02 ± 0.00
	60–70	0.12 ± 0.05	0.06 ± 0.02	0.05 ± 0.02	0.10 ± 0.03	0.10 ± 0.01	0.06 ± 0.02	0.02 ± 0.02
	70–80	0.11 ± 0.05	0.03 ± 0.01	0.05 ± 0.01	0.09 ± 0.02	0.13 ± 0.02	0.06 ± 0.02	0.02 ± 0.01
	80–90	0.10 ± 0.02	0.01 ± 0.01	0.01 ± 0.01	0.01 ± 0.01	0.01 ± 0.02	0.05 ± 0.03	0.01 ± 0.00
	90–100	0.06 ± 0.01	0.00 ± 0.00	0.00 ± 0.00	0.01 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
	Topsoil (0–30cm)	2.04 ± 0.53	2.00 ± 1.33	0.56 ± 0.18	1.72 ± 0.51	2.44 ± 0.34	3.00 ± 0.78	0.16 ± 0.11
	Subsoil (30–100cm)	0.78 ± 0.16	0.33 ± 0.09	0.30 ± 0.04	0.61 ± 0.16	0.73 ± 0.05	0.50 ± 0.14	0.16 ± 0.05
	Total (0–100cm)	2.82 ± 0.61	2.33 ± 1.36	0.86 ± 0.15	2.26 ± 0.35	3.17 ± 0.37	3.50 ± 0.66	1.77 ± 0.58
Total Root Length (cm)	0–10	1957 ± 389	1931 ± 1053	1081 ± 157	2462 ± 615	4295 ± 1023	3947 ± 1197	1332 ± 351
	10–20	2020 ± 575	1004 ± 384	705 ± 43	1534 ± 294	1770 ± 546	1168 ± 265	701 ± 162
	20–30	2173 ± 127	1102 ± 199	749 ± 333	1548 ± 199	2256 ± 775	1193 ± 353	724 ± 213
	30–40	1169 ± 175	619 ± 152	502 ± 312	875 ± 180	1020 ± 159	833 ± 448	292 ± 241
	40–50	1093 ± 195	613 ± 139	525 ± 252	984 ± 702	1028 ± 372	707 ± 23	254 ± 81
	50–60	1375 ± 572	660 ± 106	421 ± 133	1149 ± 240	1012 ± 205	695 ± 172	248 ± 204
	60–70	1293 ± 126	449 ± 139	370 ± 135	952 ± 84	1063 ± 200	663 ± 189	244 ± 17
	70–80	1284 ± 649	217 ± 173	338 ± 351	908 ± 158	817 ± 557	705 ± 188	217 ± 98
	80–90	1133 ± 203	21 ± 11	17 ± 39	418 ± 111	860 ± 109	637 ± 261	98 ± 102
	90–100	670 ± 514	16 ± 8	10 ± 4	4 ± 61	579 ± 301	397 ± 190	12 ± 5
	Topsoil (0–30cm)	8019 ± 718	4037 ± 1249	2535 ± 477	5544 ± 721	8320 ± 1943	6307 ± 1693	2757 ± 1693
	Subsoil (30–100cm)	8018 ± 1680	2594 ± 390	2253 ± 381	5376 ± 1246	6380 ± 1674	4728 ± 1385	1325 ± 1165
	Total (0–100cm)	16037 ± 1463	6631 ± 1262	4787 ± 365	10921 ± 1320	14699 ± 1966	11036 ± 914	4122 ± 556
RLD (cm cm^{-3})	0–10	6.11 ± 0.97	3.04 ± 1.65	1.70 ± 0.25	3.87 ± 0.97	6.75 ± 1.61	6.20 ± 1.88	2.09 ± 0.25
	10–20	3.08 ± 0.55	1.58 ± 0.60	1.11 ± 0.07	2.41 ± 0.46	2.78 ± 0.86	1.84 ± 0.42	1.10 ± 0.25
	20–30	3.42 ± 0.20	1.73 ± 0.31	1.18 ± 0.52	2.43 ± 0.31	3.55 ± 1.22	1.87 ± 0.56	1.14 ± 0.33
	30–40	1.84 ± 0.28	0.97 ± 0.24	0.79 ± 0.49	1.38 ± 0.18	1.62 ± 0.25	1.31 ± 0.70	0.46 ± 0.35
	40–50	1.72 ± 0.31	0.96 ± 0.33	0.83 ± 0.40	1.50 ± 0.74	1.62 ± 0.58	1.25 ± 0.12	0.40 ± 0.13
	50–60	2.16 ± 0.90	1.04 ± 0.22	0.66 ± 0.21	1.81 ± 0.38	1.59 ± 0.32	1.09 ± 0.31	0.39 ± 0.32
	60–70	2.03 ± 0.20	0.71 ± 0.17	0.58 ± 0.21	1.50 ± 0.13	1.67 ± 0.31	1.04 ± 0.30	0.38 ± 0.29
	70–80	2.02 ± 1.02	0.34 ± 0.27	0.53 ± 0.55	1.43 ± 0.25	1.28 ± 0.88	1.11 ± 0.30	0.34 ± 0.29
	80–90	1.79 ± 0.32	0.03 ± 0.02	0.03 ± 0.06	0.66 ± 0.17	1.35 ± 0.17	1.00 ± 0.41	0.15 ± 0.16
	90–100	1.05 ± 0.81	0.02 ± 0.01	0.02 ± 0.01	0.14 ± 0.10	0.91 ± 0.47	0.62 ± 0.30	0.02 ± 0.01
	Topsoil (0–30cm)	4.20 ± 0.38	2.12 ± 0.65	1.33 ± 0.25	2.91 ± 0.38	4.36 ± 1.02	3.30 ± 0.89	1.44 ± 0.23

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Trait	Layer	NPKCa+m+s	NPKCa	_PKCa	N_KCa	NP_Ca	NPK_	Unfertilized
	Subsoil (30–100cm)	1.80 ± 0.38	0.58 ± 0.09	0.51 ± 0.09	1.21 ± 0.28	1.43 ± 0.31	1.08 ± 0.25	0.31 ± 0.08
	Total (0–100cm)	2.52 ± 0.23	1.04 ± 0.20	0.75 ± 0.06	1.72 ± 0.21	2.31 ± 0.31	1.72 ± 0.34	0.65 ± 0.19
RMD (mg cm^{-3})	0–10	1.56 ± 0.52	1.74 ± 1.33	0.41 ± 0.17	1.34 ± 0.54	2.00 ± 0.23	2.55 ± 0.69	1.42 ± 0.58
	10–20	0.20 ± 0.04	0.14 ± 0.03	0.08 ± 0.03	0.18 ± 0.04	0.19 ± 0.10	0.23 ± 0.05	0.10 ± 0.01
	20–30	0.28 ± 0.03	0.12 ± 0.01	0.07 ± 0.03	0.20 ± 0.03	0.26 ± 0.09	0.23 ± 0.06	0.10 ± 0.04
	30–40	0.13 ± 0.04	0.07 ± 0.00	0.02 ± 0.02	0.10 ± 0.03	0.13 ± 0.04	0.12 ± 0.05	0.05 ± 0.03
	40–50	0.12 ± 0.03	0.06 ± 0.02	0.07 ± 0.03	0.08 ± 0.02	0.09 ± 0.01	0.06 ± 0.02	0.03 ± 0.01
	50–60	0.13 ± 0.06	0.09 ± 0.03	0.07 ± 0.01	0.09 ± 0.02	0.11 ± 0.02	0.07 ± 0.03	0.03 ± 0.00
	60–70	0.12 ± 0.05	0.06 ± 0.02	0.05 ± 0.02	0.10 ± 0.02	0.10 ± 0.01	0.06 ± 0.02	0.02 ± 0.02
	70–80	0.11 ± 0.05	0.03 ± 0.04	0.05 ± 0.03	0.10 ± 0.02	0.13 ± 0.02	0.06 ± 0.02	0.02 ± 0.03
	80–90	0.10 ± 0.02	0.01 ± 0.01	0.01 ± 0.01	0.05 ± 0.03	0.11 ± 0.01	0.06 ± 0.03	0.01 ± 0.01
	90–100	0.06 ± 0.00	0.00 ± 0.00	0.00 ± 0.01	0.01 ± 0.03	0.03 ± 0.00	0.01 ± 0.01	0.01 ± 0.00
	Topsoil (0–30cm)	0.68 ± 0.17	0.67 ± 0.44	0.19 ± 0.06	0.57 ± 0.17	0.82 ± 0.11	1.00 ± 0.26	0.54 ± 0.18
	Subsoil (30–100cm)	0.11 ± 0.02	0.05 ± 0.01	0.04 ± 0.01	0.08 ± 0.02	0.10 ± 0.01	0.07 ± 0.02	0.04 ± 0.01
	Total (0–100cm)	0.28 ± 0.06	0.23 ± 0.14	0.09 ± 0.02	0.23 ± 0.04	0.32 ± 0.04	0.35 ± 0.07	0.18 ± 0.06
Average Diameter (mm)	0–10	0.30 ± 0.04	0.39 ± 0.12	0.31 ± 0.05	0.34 ± 0.05	0.35 ± 0.05	0.38 ± 0.02	0.46 ± 0.12
	10–20	0.21 ± 0.01	0.23 ± 0.00	0.21 ± 0.01	0.23 ± 0.01	0.22 ± 0.01	0.28 ± 0.01	0.22 ± 0.02
	20–30	0.22 ± 0.02	0.23 ± 0.02	0.21 ± 0.02	0.23 ± 0.01	0.23 ± 0.01	0.29 ± 0.03	0.24 ± 0.02
	30–40	0.22 ± 0.01	0.23 ± 0.01	0.22 ± 0.01	0.24 ± 0.02	0.22 ± 0.02	0.25 ± 0.02	0.28 ± 0.05
	40–50	0.21 ± 0.01	0.21 ± 0.02	0.20 ± 0.01	0.23 ± 0.02	0.21 ± 0.01	0.22 ± 0.01	0.21 ± 0.03
	50–60	0.21 ± 0.02	0.22 ± 0.01	0.21 ± 0.01	0.22 ± 0.03	0.22 ± 0.01	0.21 ± 0.02	0.20 ± 0.03
	60–70	0.22 ± 0.01	0.22 ± 0.02	0.23 ± 0.01	0.22 ± 0.03	0.25 ± 0.01	0.21 ± 0.02	0.22 ± 0.02
	70–80	0.22 ± 0.01	0.22 ± 0.01	0.22 ± 0.02	0.22 ± 0.03	0.22 ± 0.01	0.21 ± 0.02	0.20 ± 0.01
	80–90	0.21 ± 0.02	0.23 ± 0.01	0.22 ± 0.02	0.22 ± 0.03	0.26 ± 0.03	0.21 ± 0.01	0.21 ± 0.01
	90–100	0.21 ± 0.02	0.26 ± 0.05	0.25 ± 0.01	0.23 ± 0.02	0.27 ± 0.02	0.23 ± 0.03	0.31 ± 0.13
	Topsoil (0–30cm)	0.24 ± 0.02	0.28 ± 0.04	0.24 ± 0.01	0.27 ± 0.02	0.26 ± 0.02	0.32 ± 0.01	0.31 ± 0.04
	Subsoil (30–100cm)	0.21 ± 0.01	0.23 ± 0.01	0.22 ± 0.00	0.23 ± 0.02	0.24 ± 0.00	0.22 ± 0.01	0.23 ± 0.03
	Total (0–100cm)	0.22 ± 0.01	0.24 ± 0.01	0.23 ± 0.01	0.24 ± 0.01	0.24 ± 0.01	0.25 ± 0.01	0.26 ± 0.03

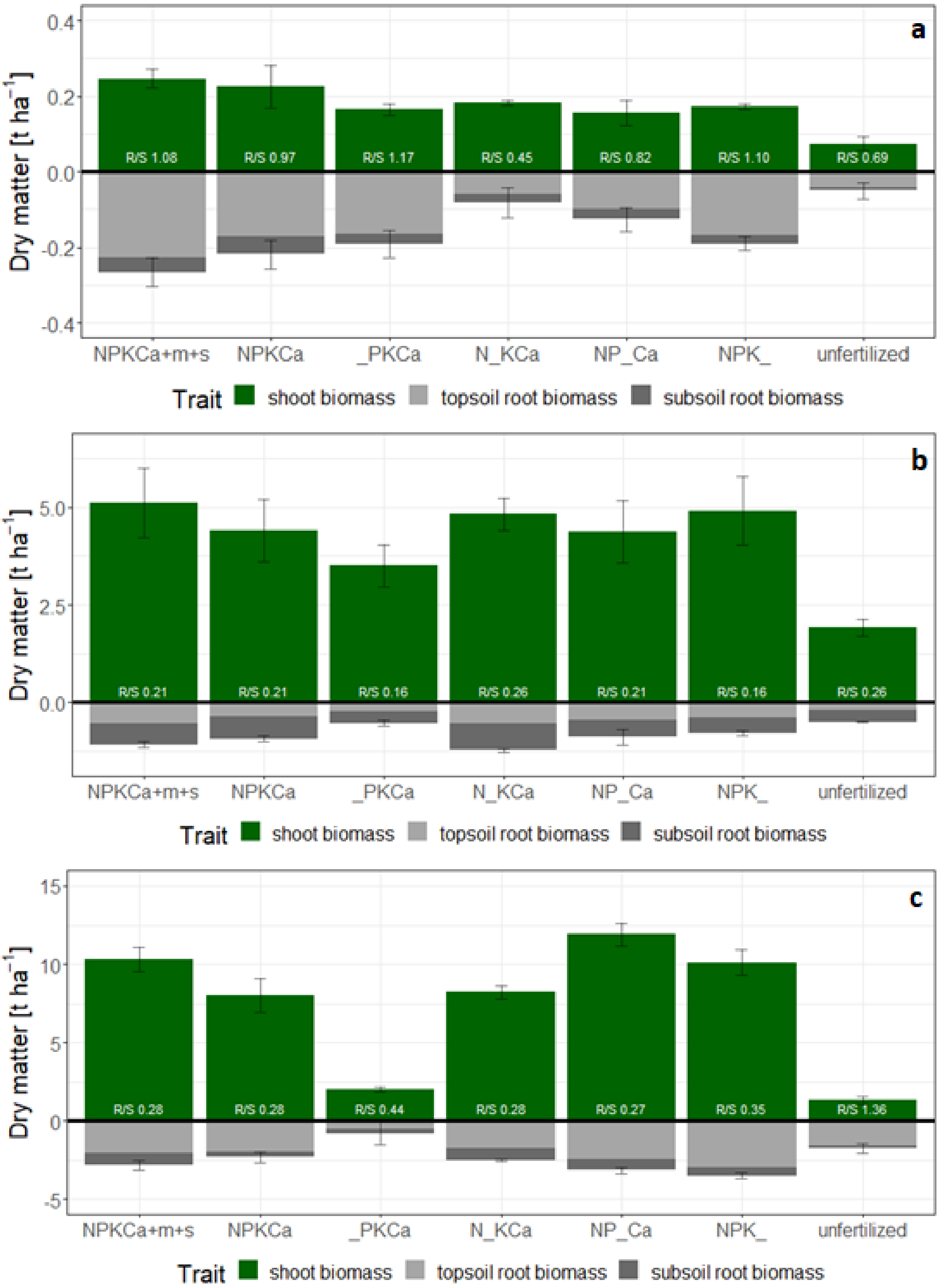

Figure B.4: Mean (n=4) shoot and root biomass (topsoil: 0–30 cm; subsoil: 30–100 cm), root-to-shoot ratio (R/S) at seven treatments at the LTFE Dikopshof, Germany. (a) growing period 1 (2019/20 – BBCH 23), (b) growing period 1 (2019/20 – BBCH 43), and (c) growing period 2 (2020/21 – BBCH 69). Error bars refer to the standard error.

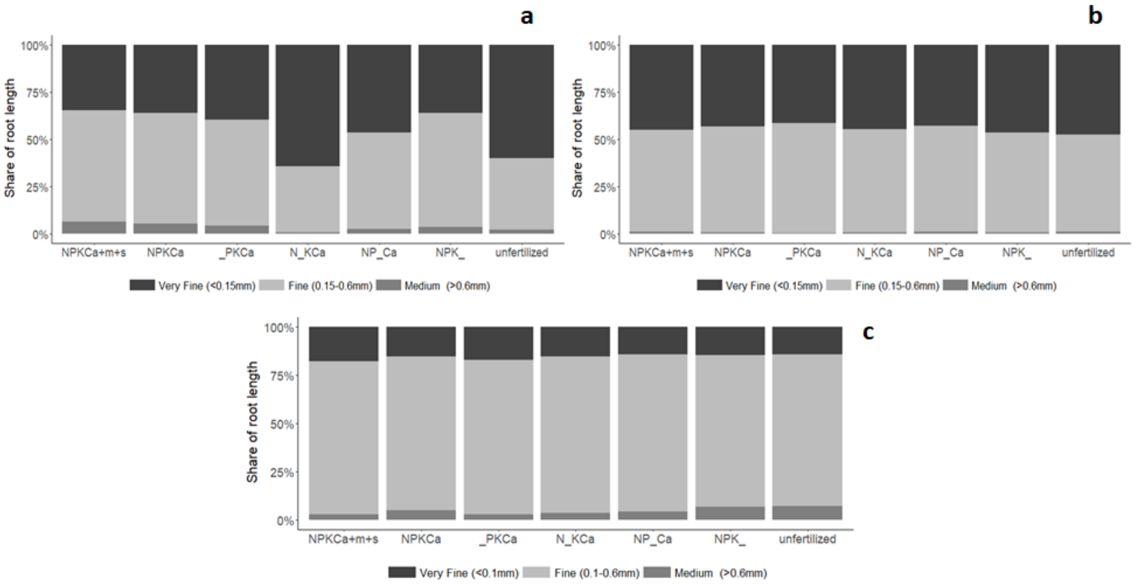

Figure B.5: Observed mean (n=4) root length distribution based on average diameter in seven treatments of the LTFE Dikopshof, Germany in (a) growing period 1 (2019/20 – BBCH 23), (b) growing period 1 (2019/20 – BBCH 43), and (c) growing period 2 (2020/21 – BBCH 69).

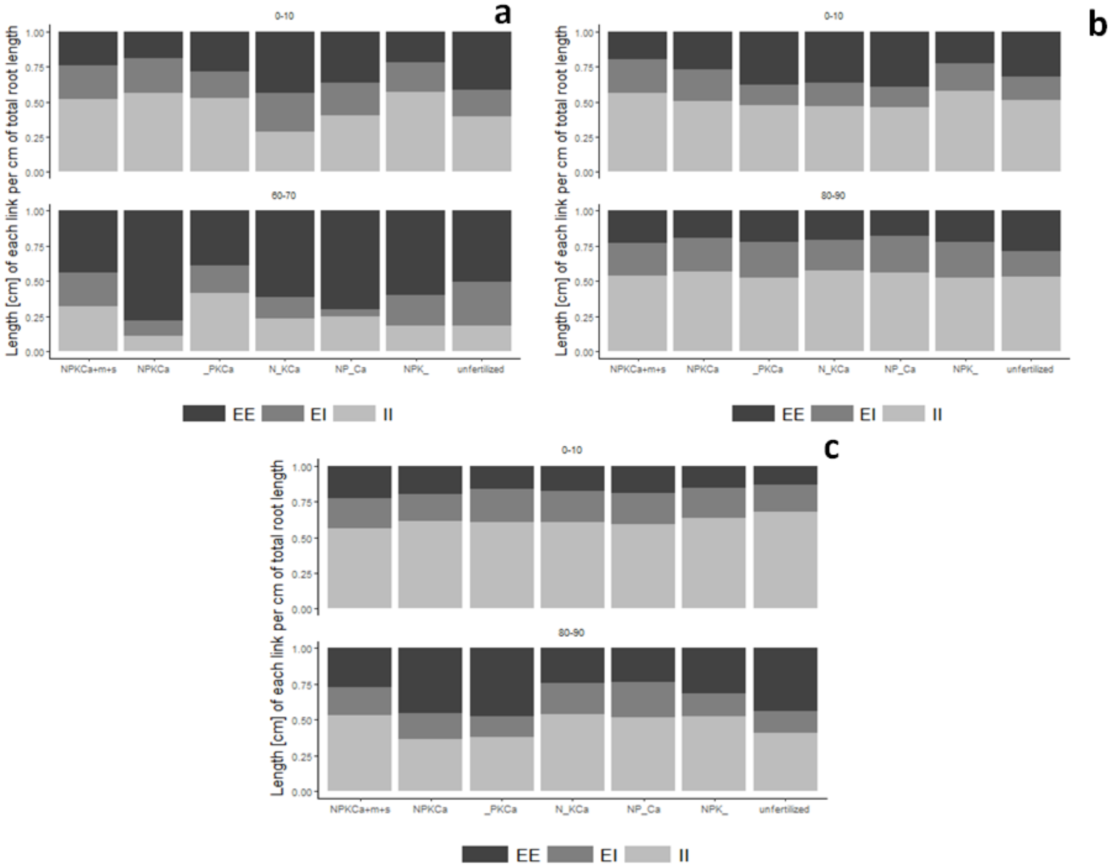

Figure B.6: Link analysis: Share of root link type at the topsoil (0–10 cm) and subsoil (either 60–70 cm at BBCH 23 or 80–89 cm at BBCH 43) in seven treatments of the LTFE Dikopshof, Germany in growing period 1 (2019/20) at (a) BBCH 23, (b) BBCH 43, and growing period 2 (2020/21) at (c) BBCH 69. Link types EE: external-external, EI: external-internal, II: internal-internal.

Table B.9: Link analysis (BBCH 23) - Period 1 (2019-2020)

Layer	Root T	NPKCa+m+s	NPKCa	_PKCa	N_KCa	NP_Ca	NPK_	Unfertilized
0-10	%EE	0.24 ± 0.10	0.19 ± 0.06	0.29 ± 0.23	0.44 ± 0.14	0.37 ± 0.13	0.22 ± 0.08	0.42 ± 0.19
	%EI	0.24 ± 0.01	0.25 ± 0.03	0.19 ± 0.02	0.27 ± 0.12	0.23 ± 0.05	0.21 ± 0.03	0.19 ± 0.07
	%II	0.52 ± 0.10	0.56 ± 0.08	0.52 ± 0.24	0.29 ± 0.06	0.40 ± 0.16	0.57 ± 0.06	0.39 ± 0.13
60-70	%EE	0.44 ± 0.38	0.78 ± 0.36	0.39 ± 0.44	0.61 ± 0.31	0.70 ± 0.30	0.60 ± 0.28	0.50 ± 0.35
	%EI	0.24 ± 0.26	0.11 ± 0.21	0.20 ± 0.17	0.15 ± 0.26	0.05 ± 0.06	0.22 ± 0.21	0.32 ± 0.38
	%II	0.32 ± 0.12	0.11 ± 0.15	0.41 ± 0.30	0.24 ± 0.09	0.25 ± 0.23	0.18 ± 0.17	0.18 ± 0.11

Table B.10: Link analysis (BBCH 43) - Period 1 (2019-2020)

Layer	Root T	NPKCa+m+s	NPKCa	_PKCa	N_KCa	NP_Ca	NPK_	Unfertilized
0-10	%EE	0.20 ± 0.06	0.27 ± 0.07	0.38 ± 0.10	0.37 ± 0.21	0.39 ± 0.19	0.23 ± 0.08	0.32 ± 0.09
	%EI	0.24 ± 0.05	0.23 ± 0.04	0.15 ± 0.06	0.17 ± 0.07	0.15 ± 0.08	0.20 ± 0.03	0.17 ± 0.04
	%II	0.57 ± 0.06	0.51 ± 0.08	0.47 ± 0.07	0.47 ± 0.14	0.46 ± 0.14	0.58 ± 0.09	0.51 ± 0.09
80-90	%EE	0.23 ± 0.14	0.20 ± 0.07	0.23 ± 0.08	0.21 ± 0.05	0.18 ± 0.07	0.22 ± 0.04	0.29 ± 0.08
	%EI	0.24 ± 0.09	0.24 ± 0.09	0.25 ± 0.06	0.22 ± 0.04	0.26 ± 0.08	0.26 ± 0.09	0.18 ± 0.06
	%II	0.54 ± 0.10	0.57 ± 0.04	0.52 ± 0.07	0.58 ± 0.05	0.56 ± 0.04	0.53 ± 0.05	0.54 ± 0.03

Table B.11: Link analysis (BBCH 69) - Period 2 (2020-2021)

Layer	Root Type	NPKCa+m+s	NPKCa	_PKCa	N_KCa	NP_Ca	NPK_	Unfertilized
0-10	%EE	0.23 ± 0.08	0.20 ± 0.02	0.16 ± 0.09	0.18 ± 0.07	0.20 ± 0.04	0.20 ± 0.06	0.19 ± 0.04
	%EI	0.21 ± 0.03	0.19 ± 0.01	0.23 ± 0.02	0.22 ± 0.02	0.21 ± 0.01	0.21 ± 0.03	0.19 ± 0.04
	%II	0.56 ± 0.07	0.61 ± 0.02	0.61 ± 0.09	0.61 ± 0.05	0.60 ± 0.11	0.64 ± 0.08	0.67 ± 0.07
10-20	%EE	0.28 ± 0.08	0.26 ± 0.12	0.31 ± 0.12	0.39 ± 0.12	0.33 ± 0.16	0.26 ± 0.07	0.31 ± 0.17
	%EI	0.27 ± 0.03	0.22 ± 0.05	0.24 ± 0.09	0.16 ± 0.06	0.23 ± 0.05	0.21 ± 0.04	0.19 ± 0.07
	%II	0.45 ± 0.09	0.53 ± 0.10	0.45 ± 0.10	0.45 ± 0.07	0.44 ± 0.13	0.53 ± 0.05	0.50 ± 0.11
20-30	%EE	0.26 ± 0.07	0.43 ± 0.20	0.42 ± 0.21	0.30 ± 0.13	0.24 ± 0.09	0.28 ± 0.07	0.38 ± 0.10
	%EI	0.28 ± 0.04	0.20 ± 0.10	0.23 ± 0.15	0.24 ± 0.03	0.25 ± 0.06	0.22 ± 0.04	0.19 ± 0.07
	%II	0.46 ± 0.07	0.38 ± 0.12	0.35 ± 0.10	0.47 ± 0.10	0.51 ± 0.05	0.50 ± 0.07	0.43 ± 0.12
30-40	%EE	0.30 ± 0.12	0.36 ± 0.16	0.26 ± 0.03	0.43 ± 0.06	0.38 ± 0.17	0.28 ± 0.14	0.41 ± 0.11
	%EI	0.17 ± 0.03	0.20 ± 0.08	0.23 ± 0.07	0.14 ± 0.06	0.15 ± 0.13	0.22 ± 0.10	0.17 ± 0.02
	%II	0.49 ± 0.04	0.45 ± 0.10	0.52 ± 0.06	0.44 ± 0.04	0.47 ± 0.11	0.50 ± 0.06	0.42 ± 0.09
40-50	%EE	0.25 ± 0.05	0.43 ± 0.11	0.45 ± 0.24	0.35 ± 0.13	0.33 ± 0.08	0.37 ± 0.10	0.32 ± 0.09
	%EI	0.20 ± 0.10	0.18 ± 0.04	0.17 ± 0.08	0.19 ± 0.13	0.22 ± 0.04	0.15 ± 0.02	0.25 ± 0.05
	%II	0.50 ± 0.06	0.39 ± 0.11	0.39 ± 0.17	0.46 ± 0.06	0.46 ± 0.09	0.49 ± 0.08	0.44 ± 0.06
50-60	%EE	0.26 ± 0.08	0.27 ± 0.04	0.40 ± 0.10	0.31 ± 0.08	0.25 ± 0.04	0.40 ± 0.15	0.36 ± 0.15
	%EI	0.27 ± 0.11	0.16 ± 0.05	0.18 ± 0.05	0.21 ± 0.08	0.23 ± 0.03	0.17 ± 0.03	0.20 ± 0.07
	%II	0.44 ± 0.13	0.57 ± 0.08	0.43 ± 0.07	0.48 ± 0.05	0.52 ± 0.05	0.44 ± 0.16	0.44 ± 0.09
60-70	%EE	0.22 ± 0.07	0.30 ± 0.09	0.37 ± 0.06	0.36 ± 0.15	0.25 ± 0.07	0.35 ± 0.13	0.36 ± 0.17
	%EI	0.25 ± 0.04	0.18 ± 0.04	0.20 ± 0.02	0.16 ± 0.12	0.19 ± 0.03	0.18 ± 0.07	0.20 ± 0.12
	%II	0.52 ± 0.10	0.52 ± 0.12	0.43 ± 0.06	0.49 ± 0.05	0.56 ± 0.05	0.47 ± 0.08	0.44 ± 0.06
70-80	%EE	0.31 ± 0.09	0.37 ± 0.12	0.45 ± 0.11	0.31 ± 0.08	0.23 ± 0.12	0.30 ± 0.12	0.36 ± 0.15
	%EI	0.14 ± 0.01	0.20 ± 0.04	0.14 ± 0.04	0.18 ± 0.05	0.25 ± 0.14	0.21 ± 0.06	0.15 ± 0.05
	%II	0.53 ± 0.03	0.43 ± 0.09	0.41 ± 0.11	0.52 ± 0.08	0.52 ± 0.05	0.49 ± 0.08	0.50 ± 0.11
80-90	%EE	0.26 ± 0.12	0.45 ± 0.19	0.48 ± 0.04	0.24 ± 0.09	0.24 ± 0.05	0.32 ± 0.06	0.44 ± 0.19

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Layer	Root Type	NPKCa+m+s	NPKCa	_PKCa	N_KCa	NP_Ca	NPK_	Unfertilized
	%EI	0.19 ± 0.08	0.18 ± 0.08	0.15 ± 0.07	0.22 ± 0.07	0.25 ± 0.11	0.16 ± 0.06	0.15 ± 0.10
	%II	0.52 ± 0.06	0.37 ± 0.13	0.38 ± 0.08	0.54 ± 0.03	0.52 ± 0.10	0.52 ± 0.04	0.41 ± 0.12
90-100	%EE	0.23 ± 0.11	0.59 ± 0.24	0.69 ± 0.35	0.49 ± 0.32	0.32 ± 0.13	0.25 ± 0.10	0.68 ± 0.39
	%EI	0.27 ± 0.05	0.16 ± 0.12	0.07 ± 0.10	0.15 ± 0.11	0.16 ± 0.05	0.22 ± 0.02	0.14 ± 0.22
	%II	0.49 ± 0.08	0.26 ± 0.16	0.24 ± 0.26	0.36 ± 0.23	0.52 ± 0.11	0.53 ± 0.11	0.18 ± 0.19

Table B.12: Shoot traits - Period 1 (2019-2020)

Samp. Date	Treatment	BBCH	Dry biomass (t ha^{-1})	LAI (m^2 m^{-2})	Height (cm)
17-Mar-20	NPKCa+m+s	23	0.25 ± 0.02	0.31 ± 0.03	6.2 ± 0.6
	NPKCa	23	0.23 ± 0.06	0.26 ± 0.03	5.3 ± 0.5
	_PKCa	23	0.16 ± 0.01	0.21 ± 0.02	5.1 ± 0.4
	N_KCa	23	0.19 ± 0.01	0.22 ± 0.02	4.6 ± 1.0
	NP_Ca	23	0.16 ± 0.03	0.19 ± 0.04	5.0 ± 0.5
	NPK_	23	0.17 ± 0.01	0.21 ± 0.01	6.2 ± 0.6
	Unfertilized	23	0.07 ± 0.02	0.09 ± 0.03	5.0 ± 0.2
30-Mar-20	NPKCa+m+s	24			8.2 ± 1.0
	NPKCa	24			6.4 ± 0.9
	_PKCa	23			6.4 ± 0.9
	N_KCa	24			6.0 ± 0.8
	NP_Ca	24			6.1 ± 0.9
	NPK_	24			7.2 ± 1.2
	Unfertilized	23			5.3 ± 0.8
7-Apr-20	NPKCa+m+s	25	0.83 ± 0.11	0.99 ± 0.17	
	NPKCa	24	0.54 ± 0.08	0.56 ± 0.03	
	_PKCa	24	0.43 ± 0.03	0.44 ± 0.03	
	N_KCa	24	0.52 ± 0.04	0.54 ± 0.03	
	NP_Ca	24	0.58 ± 0.04	0.61 ± 0.05	
	NPK_	25	0.61 ± 0.12	0.59 ± 0.16	
	Unfertilized	24	0.22 ± 0.08	0.21 ± 0.07	
22-Apr-20	NPKCa+m+s	31	1.86 ± 0.09	1.86 ± 0.14	20.7 ± 2.8
	NPKCa	31	1.16 ± 0.11	1.07 ± 0.12	14.5 ± 1.2
	_PKCa	31	0.86 ± 0.08	0.82 ± 0.07	11.5 ± 1.0
	N_KCa	31	1.29 ± 0.05	1.22 ± 0.06	13.2 ± 1.5
	NP_Ca	31	1.12 ± 0.15	1.08 ± 0.15	12.3 ± 1.8
	NPK_	31	1.14 ± 0.29	0.98 ± 0.26	14.9 ± 1.8
	Unfertilized	31	0.43 ± 0.18	0.41 ± 0.16	9.2 ± 1.4
7-May-20	NPKCa+m+s	37	4.87 ± 0.36	3.89 ± 0.29	43.0 ± 4.0
	NPKCa	37	2.77 ± 0.37	1.84 ± 0.25	33.4 ± 0.3
	_PKCa	37	2.06 ± 0.12	1.35 ± 0.05	26.7 ± 1.3
	N_KCa	37	3.35 ± 0.45	2.17 ± 0.26	30.2 ± 2.5
	NP_Ca	37	2.89 ± 0.61	1.96 ± 0.49	31.7 ± 2.5
	NPK_	37	2.77 ± 0.31	1.72 ± 0.18	34.6 ± 1.1
	Unfertilized	32	0.58 ± 0.34	0.34 ± 0.12	20.9 ± 1.8
19-May-20	NPKCa+m+s	43	5.11 ± 0.89	2.28 ± 0.36	54.3 ± 4.3
	NPKCa	43	4.40 ± 0.80	1.68 ± 0.25	45.5 ± 1.4
	_PKCa	43	3.51 ± 0.54	1.15 ± 0.21	36.8 ± 0.9
	N_KCa	45	4.83 ± 0.42	1.82 ± 0.11	45.5 ± 3.4
	NP_Ca	43	4.38 ± 0.81	1.72 ± 0.25	43.6 ± 1.1
	NPK_	43	4.91 ± 0.87	1.94 ± 0.33	48.7 ± 2.8
	Unfertilized	39	1.91 ± 0.22	0.74 ± 0.05	35.4 ± 2.8
2-Jun-20	NPKCa+m+s	69			65.2 ± 3.6
	NPKCa	69			56.3 ± 1.3
	_PKCa	69			46.7 ± 0.6
	N_KCa	69			59.9 ± 2.3
	NP_Ca	69			57.3 ± 2.2
	NPK_	69			60.5 ± 4.0

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Sampling Date	Treatment	BBCH	Dry biomass (t ha^{-1})	LAI (m^2 m^{-2})	Height (cm)
	Unfertilized	65			48.8 ± 5.2
17-Jun-20	NPKCa+m+s	83			67.1 ± 1.5
	NPKCa	83			56.3 ± 1.3
	_PKCa	83			44.7 ± 3.7
	N_KCa	84			58.4 ± 1.1
	NP_Ca	84			58.2 ± 1.9
	NPK_	84			60.7 ± 3.3
	Unfertilized	84			50.2 ± 1.9

Table B.13: Plant (plants/m^2) and ear (ears/m^2) densities recorded at different growth stages (BBCH 23-28, BBCH 65, and BBCH 69) for two growing periods (GP 1: 2019/20 and GP 2: 2020/21).

	GP 1 (2019/20)		GP 2 (2020/21)	
Treatment	BBCH 23-28 plants/m^2	BBCH 65 ears/m^2	BBCH 69 tillers/m^2	BBCH 69 ears/m^2
NPKCa+m+s	131	467	345	345
NPKCa	151	420	251	246
_PKCa	119	267	135	133
N_KCa	126	427	295	283
NP_Ca	135	520	342	318
NPK_	102	454	294	292
unfertilized	54	158	167	130

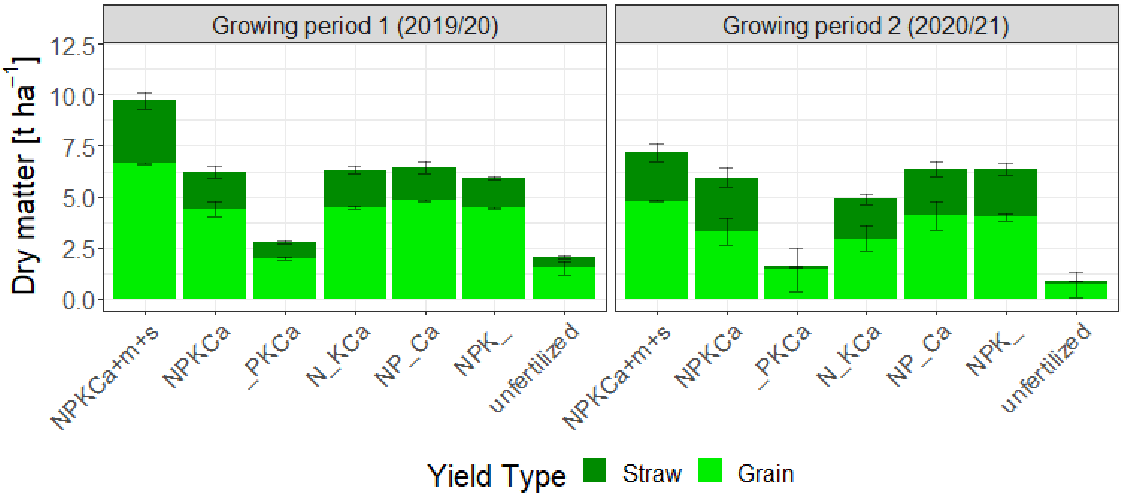

Figure B.7: Observed dry matter grain and straw yield of winter wheat cultivated in the seven treatments of the LTFE Dikopshof, Germany, in growing period 1 (2019/20) and growing period 2 (2020/21). Error bars refer to the standard error.

Table B.14: Data used for Pearson Correlation test: Part I

treatment	year	bbch	N_level	P_level	K_level	Ca_level	pH_topsoil	C_topsoil	N_topsoil	Nmin_topsoil	Kcal_topsoil	Pcal_topsoil
NPKCa+m+s	2020	23	120	31	116	1	6.64	1.23	0.11	13.80	353.53	173.51
NPKCa+m+s	2020	23	120	31	116	1	6.64	1.23	0.11	13.80	353.53	173.51
NPKCa+m+s	2020	23	120	31	116	1	6.64	1.23	0.11	13.80	353.53	173.51
NPKCa+m+s	2020	23	120	31	116	1	6.64	1.23	0.11	13.80	353.53	173.51
NPKCa	2020	23	60	31	116	1	6.76	0.87	0.08	6.80	163.79	119.01
NPKCa	2020	23	60	31	116	1	6.76	0.87	0.08	6.80	163.79	119.01
NPKCa	2020	23	60	31	116	1	6.76	0.87	0.08	6.80	163.79	119.01
NPKCa	2020	23	60	31	116	1	6.76	0.87	0.08	6.80	163.79	119.01
_PKCa	2020	23	0	31	116	1	6.82	0.77	0.07	7.00	161.21	128.89
_PKCa	2020	23	0	31	116	1	6.82	0.77	0.07	7.00	161.21	128.89
_PKCa	2020	23	0	31	116	1	6.82	0.77	0.07	7.00	161.21	128.89
_PKCa	2020	23	0	31	116	1	6.82	0.77	0.07	7.00	161.21	128.89
N_KCa	2020	23	60	0	116	1	6.84	0.80	0.07	4.73	110.70	25.44
N_KCa	2020	23	60	0	116	1	6.84	0.80	0.07	4.73	110.70	25.44
N_KCa	2020	23	60	0	116	1	6.84	0.80	0.07	4.73	110.70	25.44
N_KCa	2020	23	60	0	116	1	6.84	0.80	0.07	4.73	110.70	25.44
NP_Ca	2020	23	60	31	0	1	6.77	0.75	0.07	5.62	38.09	110.45
NP_Ca	2020	23	60	31	0	1	6.77	0.75	0.07	5.62	38.09	110.45
NP_Ca	2020	23	60	31	0	1	6.77	0.75	0.07	5.62	38.09	110.45
NP_Ca	2020	23	60	31	0	1	6.77	0.75	0.07	5.62	38.09	110.45
NPK_	2020	23	60	31	116	0	6.52	0.79	0.07	3.92	62.16	114.33
NPK_	2020	23	60	31	116	0	6.52	0.79	0.07	3.92	62.16	114.33
NPK_	2020	23	60	31	116	0	6.52	0.79	0.07	3.92	62.16	114.33
NPK_	2020	23	60	31	116	0	6.52	0.79	0.07	3.92	62.16	114.33
unfertilized	2020	23	0	0	0	0	5.81	0.74	0.07	4.82	48.00	30.35
unfertilized	2020	23	0	0	0	0	5.81	0.74	0.07	4.82	48.00	30.35
unfertilized	2020	23	0	0	0	0	5.81	0.74	0.07	4.82	48.00	30.35
unfertilized	2020	23	0	0	0	0	5.81	0.74	0.07	4.82	48.00	30.35
NPKCa+m+s	2020	43	120	31	116	1	6.57	1.27	0.12	25.99	417.09	201.09
NPKCa+m+s	2020	43	120	31	116	1	6.57	1.27	0.12	25.99	417.09	201.09
NPKCa+m+s	2020	43	120	31	116	1	6.57	1.27	0.12	25.99	417.09	201.09
NPKCa+m+s	2020	43	120	31	116	1	6.57	1.27	0.12	25.99	417.09	201.09
NPKCa	2020	43	60	31	116	1	6.70	0.78	0.07	12.96	111.79	116.90
NPKCa	2020	43	60	31	116	1	6.70	0.78	0.07	12.96	111.79	116.90
NPKCa	2020	43	60	31	116	1	6.70	0.78	0.07	12.96	111.79	116.90
NPKCa	2020	43	60	31	116	1	6.70	0.78	0.07	12.96	111.79	116.90
_PKCa	2020	43	0	31	116	1	6.84	0.81	0.07	5.10	205.69	61.49
_PKCa	2020	43	0	31	116	1	6.84	0.81	0.07	5.10	205.69	61.49

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Table B.14: Data used for Pearson Correlation test: Part I (Continued)

treatment	year	bbch	N_level	P_level	K_level	Ca_level	pH_topsoil	C_topsoil	N_topsoil	Nmin_topsoil	Kcal_topsoil	Pcal_topsoil
_PKCa	2020	43	0	31	116	1	6.84	0.81	0.07	5.10	205.69	61.49
_PKCa	2020	43	0	31	116	1	6.84	0.81	0.07	5.10	205.69	61.49
N_KCa	2020	43	60	0	116	1	6.76	0.80	0.08	11.77	89.72	42.89
N_KCa	2020	43	60	0	116	1	6.76	0.80	0.08	11.77	89.72	42.89
N_KCa	2020	43	60	0	116	1	6.76	0.80	0.08	11.77	89.72	42.89
N_KCa	2020	43	60	0	116	1	6.76	0.80	0.08	11.77	89.72	42.89
NP_Ca	2020	43	60	31	0	1	6.11	0.56	0.06	18.37	60.88	116.34
NP_Ca	2020	43	60	31	0	1	6.11	0.56	0.06	18.37	60.88	116.34
NP_Ca	2020	43	60	31	0	1	6.11	0.56	0.06	18.37	60.88	116.34
NP_Ca	2020	43	60	31	0	1	6.11	0.56	0.06	18.37	60.88	116.34
NPK_	2020	43	60	31	116	0	5.51	0.75	0.07	12.09	79.09	63.17
NPK_	2020	43	60	31	116	0	5.51	0.75	0.07	12.09	79.09	63.17
NPK_	2020	43	60	31	116	0	5.51	0.75	0.07	12.09	79.09	63.17
NPK_	2020	43	60	31	116	0	5.51	0.75	0.07	12.09	79.09	63.17
unfertilized	2020	43	0	0	0	0	5.88	0.71	0.07	4.62	40.80	19.30
unfertilized	2020	43	0	0	0	0	5.88	0.71	0.07	4.62	40.80	19.30
unfertilized	2020	43	0	0	0	0	5.88	0.71	0.07	4.62	40.80	19.30
unfertilized	2020	43	0	0	0	0	5.88	0.71	0.07	4.62	40.80	19.30
NPKCa+m+s	2021	69	120	31	116	1	6.47	1.18	0.11	8.54	329.39	215.21
NPKCa+m+s	2021	69	120	31	116	1	6.47	1.18	0.11	8.54	329.39	215.21
NPKCa+m+s	2021	69	120	31	116	1	6.47	1.18	0.11	8.54	329.39	215.21
NPKCa+m+s	2021	69	120	31	116	1	6.47	1.18	0.11	8.54	329.39	215.21
NPKCa	2021	69	60	31	116	1	6.35	0.83	0.09	4.68	127.67	95.02
NPKCa	2021	69	60	31	116	1	6.35	0.83	0.09	4.68	127.67	95.02
NPKCa	2021	69	60	31	116	1	6.35	0.83	0.09	4.68	127.67	95.02
NPKCa	2021	69	60	31	116	1	6.35	0.83	0.09	4.68	127.67	95.02
_PKCa	2021	69	0	31	116	1	6.64	0.73	0.08	2.21	152.12	95.28
_PKCa	2021	69	0	31	116	1	6.64	0.73	0.08	2.21	152.12	95.28
_PKCa	2021	69	0	31	116	1	6.64	0.73	0.08	2.21	152.12	95.28
_PKCa	2021	69	0	31	116	1	6.64	0.73	0.08	2.21	152.12	95.28
N_KCa	2021	69	60	0	116	1	6.25	0.81	0.08	4.41	107.00	20.66
N_KCa	2021	69	60	0	116	1	6.25	0.81	0.08	4.41	107.00	20.66
N_KCa	2021	69	60	0	116	1	6.25	0.81	0.08	4.41	107.00	20.66
N_KCa	2021	69	60	0	116	1	6.25	0.81	0.08	4.41	107.00	20.66
NP_Ca	2021	69	60	31	0	1	6.06	0.74	0.08	2.26	30.60	73.69
NP_Ca	2021	69	60	31	0	1	6.06	0.74	0.08	2.26	30.60	73.69
NP_Ca	2021	69	60	31	0	1	6.06	0.74	0.08	2.26	30.60	73.69
NP_Ca	2021	69	60	31	0	1	6.06	0.74	0.08	2.26	30.60	73.69

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Table B.14: Data used for Pearson Correlation test: Part I (Continued)

treatment	year	bbch	N_level	P_level	K_level	Ca_level	pH_topsoil	C_topsoil	N_topsoil	Nmin_topsoil	Kcal_topsoil	Pcal_topsoil
NPK_	2021	69	60	31	116	0	5.46	0.75	0.08	5.43	111.08	54.04
NPK_	2021	69	60	31	116	0	5.46	0.75	0.08	5.43	111.08	54.04
NPK_	2021	69	60	31	116	0	5.46	0.75	0.08	5.43	111.08	54.04
NPK_	2021	69	60	31	116	0	5.46	0.75	0.08	5.43	111.08	54.04
unfertilized	2021	69	0	0	0	0	5.79	0.67	0.07	3.39	39.34	27.32
unfertilized	2021	69	0	0	0	0	5.79	0.67	0.07	3.39	39.34	27.32
unfertilized	2021	69	0	0	0	0	5.79	0.67	0.07	3.39	39.34	27.32
unfertilized	2021	69	0	0	0	0	5.79	0.67	0.07	3.39	39.34	27.32

Data used for Pearson Correlation test: Part II

treatment	year	pH_subsoil	C_subsoil	N_subsoil	Nmin_subsoil	Kcal_subsoil	Pcal_subpsoil	pH	C	N	Nmin
NPKCa+m+s	2020	na	na	na	na	na	na	6.64	1.23	0.11	13.80
NPKCa+m+s	2020	na	na	na	na	na	na	6.64	1.23	0.11	13.80
NPKCa+m+s	2020	na	na	na	na	na	na	6.64	1.23	0.11	13.80
NPKCa+m+s	2020	na	na	na	na	na	na	6.64	1.23	0.11	13.80
NPKCa	2020	na	na	na	na	na	na	6.76	0.87	0.08	6.80
NPKCa	2020	na	na	na	na	na	na	6.76	0.87	0.08	6.80
NPKCa	2020	na	na	na	na	na	na	6.76	0.87	0.08	6.80
NPKCa	2020	na	na	na	na	na	na	6.76	0.87	0.08	6.80
_PKCa	2020	na	na	na	na	na	na	6.82	0.77	0.07	7.00
_PKCa	2020	na	na	na	na	na	na	6.82	0.77	0.07	7.00
_PKCa	2020	na	na	na	na	na	na	6.82	0.77	0.07	7.00
_PKCa	2020	na	na	na	na	na	na	6.82	0.77	0.07	7.00
N_KCa	2020	na	na	na	na	na	na	6.84	0.80	0.07	4.73
N_KCa	2020	na	na	na	na	na	na	6.84	0.80	0.07	4.73
N_KCa	2020	na	na	na	na	na	na	6.84	0.80	0.07	4.73
N_KCa	2020	na	na	na	na	na	na	6.84	0.80	0.07	4.73
NP_Ca	2020	na	na	na	na	na	na	6.77	0.75	0.07	5.62
NP_Ca	2020	na	na	na	na	na	na	6.77	0.75	0.07	5.62
NP_Ca	2020	na	na	na	na	na	na	6.77	0.75	0.07	5.62
NP_Ca	2020	na	na	na	na	na	na	6.77	0.75	0.07	5.62
NPK_	2020	na	na	na	na	na	na	6.52	0.79	0.07	3.92
NPK_	2020	na	na	na	na	na	na	6.52	0.79	0.07	3.92
NPK_	2020	na	na	na	na	na	na	6.52	0.79	0.07	3.92

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Data used for Pearson Correlation test: Part II (Continued)

treatment	year	pH_subsoil	C_subsoil	N_subsoil	Nmin_subsoil	Kcal_subsoil	Pcal_subpsoil	pH	C	N	Nmin
NPK_	2020	na	na	na	na	na	na	6.52	0.79	0.07	3.92
unfertilized	2020	na	na	na	na	na	na	5.81	0.74	0.07	4.82
unfertilized	2020	na	na	na	na	na	na	5.81	0.74	0.07	4.82
unfertilized	2020	na	na	na	na	na	na	5.81	0.74	0.07	4.82
unfertilized	2020	na	na	na	na	na	na	5.81	0.74	0.07	4.82
NPKCa+m+s	2020	6.83	0.53	0.06	7.46	247.38	88.6	6.74	0.77	0.08	13.64
NPKCa+m+s	2020	6.83	0.53	0.06	7.46	247.38	88.6	6.74	0.77	0.08	13.64
NPKCa+m+s	2020	6.83	0.53	0.06	7.46	247.38	88.6	6.74	0.77	0.08	13.64
NPKCa+m+s	2020	6.83	0.53	0.06	7.46	247.38	88.6	6.74	0.77	0.08	13.64
NPKCa	2020	6.83	0.45	0.05	2.1	69.99	34.64	6.78	0.56	0.06	5.72
NPKCa	2020	6.83	0.45	0.05	2.1	69.99	34.64	6.78	0.56	0.06	5.72
NPKCa	2020	6.83	0.45	0.05	2.1	69.99	34.64	6.78	0.56	0.06	5.72
NPKCa	2020	6.83	0.45	0.05	2.1	69.99	34.64	6.78	0.56	0.06	5.72
_PKCa	2020	6.96	0.41	0.05	1.69	68.71	17.12	6.92	0.54	0.06	2.82
_PKCa	2020	6.96	0.41	0.05	1.69	68.71	17.12	6.92	0.54	0.06	2.82
_PKCa	2020	6.96	0.41	0.05	1.69	68.71	17.12	6.92	0.54	0.06	2.82
_PKCa	2020	6.96	0.41	0.05	1.69	68.71	17.12	6.92	0.54	0.06	2.82
N_KCa	2020	6.86	0.73	0.07	2.47	47.84	5.28	6.82	0.75	0.07	5.57
N_KCa	2020	6.86	0.73	0.07	2.47	47.84	5.28	6.82	0.75	0.07	5.57
N_KCa	2020	6.86	0.73	0.07	2.47	47.84	5.28	6.82	0.75	0.07	5.57
N_KCa	2020	6.86	0.73	0.07	2.47	47.84	5.28	6.82	0.75	0.07	5.57
NP_Ca	2020	6.44	0.29	0.04	3.85	47.15	42.5	6.33	0.38	0.05	8.69
NP_Ca	2020	6.44	0.29	0.04	3.85	47.15	42.5	6.33	0.38	0.05	8.69
NP_Ca	2020	6.44	0.29	0.04	3.85	47.15	42.5	6.33	0.38	0.05	8.69
NP_Ca	2020	6.44	0.29	0.04	3.85	47.15	42.5	6.33	0.38	0.05	8.69
NPK_	2020	6.15	0.49	0.06	5.61	49.95	10.49	5.93	0.57	0.06	7.77
NPK_	2020	6.15	0.49	0.06	5.61	49.95	10.49	5.93	0.57	0.06	7.77
NPK_	2020	6.15	0.49	0.06	5.61	49.95	10.49	5.93	0.57	0.06	7.77
NPK_	2020	6.15	0.49	0.06	5.61	49.95	10.49	5.93	0.57	0.06	7.77
unfertilized	2020	6.14	0.38	0.05	1.95	47.3	0	6.05	0.49	0.06	2.84
unfertilized	2020	6.14	0.38	0.05	1.95	47.3	0	6.05	0.49	0.06	2.84
unfertilized	2020	6.14	0.38	0.05	1.95	47.3	0	6.05	0.49	0.06	2.84
unfertilized	2020	6.14	0.38	0.05	1.95	47.3	0	6.05	0.49	0.06	2.84
NPKCa+m+s	2021	6.72	0.48	0.06	2.05	157.45	70.15	6.64	0.71	0.08	4.21
NPKCa+m+s	2021	6.72	0.48	0.06	2.05	157.45	70.15	6.64	0.71	0.08	4.21
NPKCa+m+s	2021	6.72	0.48	0.06	2.05	157.45	70.15	6.64	0.71	0.08	4.21
NPKCa+m+s	2021	6.72	0.48	0.06	2.05	157.45	70.15	6.64	0.71	0.08	4.21
NPKCa	2021	6.71	0.45	0.06	2.66	66.92	32.49	6.59	0.58	0.07	3.33

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Data used for Pearson Correlation test: Part II (Continued)

treatment	year	pH_subsoil	C_subsoil	N_subsoil	Nmin_subsoil	Kcal_subsoil	Pcal_subpsoil	pH	C	N	Nmin
NPKCa	2021	6.71	0.45	0.06	2.66	66.92	32.49	6.59	0.58	0.07	3.33
NPKCa	2021	6.71	0.45	0.06	2.66	66.92	32.49	6.59	0.58	0.07	3.33
NPKCa	2021	6.71	0.45	0.06	2.66	66.92	32.49	6.59	0.58	0.07	3.33
_PKCa	2021	6.76	0.42	0.06	1.83	71.99	32.32	6.72	0.52	0.06	1.96
_PKCa	2021	6.76	0.42	0.06	1.83	71.99	32.32	6.72	0.52	0.06	1.96
_PKCa	2021	6.76	0.42	0.06	1.83	71.99	32.32	6.72	0.52	0.06	1.96
_PKCa	2021	6.76	0.42	0.06	1.83	71.99	32.32	6.72	0.52	0.06	1.96
N_KCa	2021	6.45	0.46	0.06	2.99	59.21	12.87	6.38	0.58	0.07	3.46
N_KCa	2021	6.45	0.46	0.06	2.99	59.21	12.87	6.38	0.58	0.07	3.46
N_KCa	2021	6.45	0.46	0.06	2.99	59.21	12.87	6.38	0.58	0.07	3.46
N_KCa	2021	6.45	0.46	0.06	2.99	59.21	12.87	6.38	0.58	0.07	3.46
NP_Ca	2021	6.47	0.43	0.06	1.55	36.6	33.02	6.39	0.50	0.06	1.70
NP_Ca	2021	6.47	0.43	0.06	1.55	36.6	33.02	6.39	0.50	0.06	1.70
NP_Ca	2021	6.47	0.43	0.06	1.55	36.6	33.02	6.39	0.50	0.06	1.70
NP_Ca	2021	6.47	0.43	0.06	1.55	36.6	33.02	6.39	0.50	0.06	1.70
NPK_	2021	5.87	0.5	0.06	2.52	57.34	26.09	5.74	0.58	0.07	3.49
NPK_	2021	5.87	0.5	0.06	2.52	57.34	26.09	5.74	0.58	0.07	3.49
NPK_	2021	5.87	0.5	0.06	2.52	57.34	26.09	5.74	0.58	0.07	3.49
NPK_	2021	5.87	0.5	0.06	2.52	57.34	26.09	5.74	0.58	0.07	3.49
unfertilized	2021	5.95	0.38	0.06	2.29	41.16	12.71	5.90	0.48	0.06	2.66
unfertilized	2021	5.95	0.38	0.06	2.29	41.16	12.71	5.90	0.48	0.06	2.66
unfertilized	2021	5.95	0.38	0.06	2.29	41.16	12.71	5.90	0.48	0.06	2.66
unfertilized	2021	5.95	0.38	0.06	2.29	41.16	12.71	5.90	0.48	0.06	2.66

Data used for Pearson Correlation test: Part III

treatment	year	Kcal	Pcal	height	LAI	shoot_biomass	root_biomass	root_length	rld	rmd	diameter	root_surface
NPKCa+m+s	2020	353.53	173.51	6.70	0.27	0.21	0.23	1435.98	0.32	0.03	0.32	119.27
NPKCa+m+s	2020	353.53	173.51	6.80	0.32	0.26	0.23	2080.26	0.47	0.03	0.29	198.73
NPKCa+m+s	2020	353.53	173.51	5.65	0.33	0.25	0.38	2531.89	0.57	0.06	0.25	197.07
NPKCa+m+s	2020	353.53	173.51	5.70	0.33	0.26	0.22	2183.75	0.49	0.03	0.24	175.11
NPKCa	2020	163.79	119.01	5.60	0.22	0.21	0.19	2275.44	0.51	0.03	0.23	140.07
NPKCa	2020	163.79	119.01	5.65	0.35	0.31	0.30	2097.46	0.47	0.04	0.24	166.90
NPKCa	2020	163.79	119.01	4.65	0.25	0.20	0.12	1992.24	0.45	0.02	0.28	166.77
NPKCa	2020	163.79	119.01	5.45	0.23	0.18	0.23	1782.71	0.40	0.03	0.30	154.11

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Data used for Pearson Correlation test: Part III (Continued)

treatment	year	Kcal	Pcal	height	LAI	shoot_biomass	root_biomass	root_length	rld	rmd	diameter	root_surface
_PKCa	2020	161.21	128.89	4.90	0.24	0.19	0.22	2097.32	0.47	0.03	0.25	200.76
_PKCa	2020	161.21	128.89	4.85	0.19	0.15	0.24	2219.84	0.50	0.04	0.20	185.49
_PKCa	2020	161.21	128.89	5.60	0.21	0.16	0.07	656.81	0.15	0.01	0.19	33.26
_PKCa	2020	161.21	128.89	4.90	0.20	0.15	0.20	701.38	0.16	0.03	0.21	69.59
N_KCa	2020	110.70	25.44	4.00	0.22	0.19	0.08	376.08	0.08	0.01	0.14	16.22
N_KCa	2020	110.70	25.44	4.15	0.20	0.17	0.06	264.49	0.06	0.01	0.14	10.81
N_KCa	2020	110.70	25.44	4.20	0.22	0.18	0.03	187.67	0.04	0.01	0.14	8.57
N_KCa	2020	110.70	25.44	6.10	0.23	0.19	0.17	1039.21	0.23	0.02	0.15	61.03
NP_Ca	2020	38.09	110.45	5.25	0.17	0.14	0.07	479.56	0.11	0.01	0.15	21.83
NP_Ca	2020	38.09	110.45	4.90	0.15	0.13	0.13	378.41	0.08	0.02	0.17	18.26
NP_Ca	2020	38.09	110.45	5.60	0.25	0.20	0.15	1576.09	0.35	0.02	0.18	112.81
NP_Ca	2020	38.09	110.45	4.35	0.20	0.16	0.14	923.47	0.21	0.02	0.21	69.25
NPK_	2020	62.16	114.33	5.55	0.21	0.17	0.24	2023.00	0.45	0.03	0.25	163.86
NPK_	2020	62.16	114.33	6.90	0.20	0.17	0.26	3142.32	0.71	0.04	0.20	234.09
NPK_	2020	62.16	114.33	6.05	0.20	0.17	0.16	2104.24	0.47	0.02	0.24	170.22
NPK_	2020	62.16	114.33	6.10	0.22	0.18	0.09	1781.68	0.40	0.01	0.27	126.45
unfertilized	2020	48.00	30.35	5.30	0.12	0.10	0.05	470.67	0.11	0.01	0.22	30.70
unfertilized	2020	48.00	30.35	4.85	0.06	0.06	0.10	1017.98	0.23	0.01	0.21	64.67
unfertilized	2020	48.00	30.35	4.95	0.08	0.07	0.01	791.35	0.18	0.00	0.16	45.05
unfertilized	2020	48.00	30.35	4.75	0.08	0.07	0.02	786.29	0.18	0.00	0.16	38.05
NPKCa+m+s	2020	303.95	126.10	58.70	2.05	4.79	1.05	14272.12	2.24	0.11	0.21	916.74
NPKCa+m+s	2020	303.95	126.10	56.25	2.42	5.55	1.00	11513.05	1.81	0.10	0.22	844.21
NPKCa+m+s	2020	303.95	126.10	52.60	1.93	4.03	0.96	12886.22	2.03	0.10	0.20	877.28
NPKCa+m+s	2020	303.95	126.10	48.90	2.73	6.08	1.32	15914.41	2.50	0.13	0.21	1056.25
NPKCa	2020	83.92	62.06	44.65	1.48	3.71	0.93	9776.87	1.54	0.09	0.21	630.50
NPKCa	2020	83.92	62.06	46.95	1.71	4.45	0.79	8929.52	1.40	0.08	0.22	598.95
NPKCa	2020	83.92	62.06	43.90	1.53	3.93	0.88	10386.01	1.63	0.09	0.21	673.27
NPKCa	2020	83.92	62.06	46.45	2.02	5.50	1.15	11578.82	1.82	0.11	0.22	804.34
_PKCa	2020	114.37	31.91	38.15	0.85	2.74	0.64	6358.82	1.00	0.06	0.22	418.99
_PKCa	2020	114.37	31.91	36.50	1.17	3.56	0.58	8548.11	1.34	0.06	0.21	536.64
_PKCa	2020	114.37	31.91	36.05	1.27	3.79	0.52	11632.56	1.83	0.05	0.23	790.10
_PKCa	2020	114.37	31.91	36.55	1.31	3.96	0.41	9254.53	1.45	0.04	0.23	624.97
N_KCa	2020	61.80	17.81	49.60	1.85	4.70	0.79	8087.96	1.27	0.08	0.21	513.76
N_KCa	2020	61.80	17.81	42.40	1.80	4.89	1.24	12950.16	2.04	0.12	0.21	826.94
N_KCa	2020	61.80	17.81	42.85	1.68	4.37	1.76	18736.13	2.95	0.18	0.23	1302.94
N_KCa	2020	61.80	17.81	47.00	1.95	5.38	1.12	15417.12	2.42	0.11	0.20	977.15
NP_Ca	2020	51.72	67.11	44.05	1.40	3.17	0.85	12961.60	2.04	0.08	0.23	884.69
NP_Ca	2020	51.72	67.11	44.05	2.01	4.93	1.03	11978.81	1.88	0.10	0.23	826.91

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Data used for Pearson Correlation test: Part III (Continued)

treatment	year	Kcal	Pcal	height	LAI	shoot_biomass	root_biomass	root_length	rld	rmd	diameter	root_surface
NP_Ca	2020	51.72	67.11	44.40	1.70	4.72	0.84	12121.42	1.91	0.08	0.22	795.30
NP_Ca	2020	51.72	67.11	41.90	1.76	4.70	0.82	10928.20	1.72	0.08	0.21	722.15
NPK_	2020	59.66	28.05	45.10	2.13	5.28	0.96	10063.44	1.58	0.10	0.21	656.48
NPK_	2020	59.66	28.05	51.90	1.50	3.76	0.61	8120.56	1.28	0.06	0.20	531.51
NPK_	2020	59.66	28.05	48.20	1.96	4.81	0.78	12681.55	1.99	0.08	0.20	803.56
NPK_	2020	59.66	28.05	49.60	2.17	5.80	0.79	11131.12	1.75	0.08	0.20	699.04
unfertilized	2020	45.13	6.43	37.70	0.71	1.99	0.45	6941.26	1.09	0.05	0.21	461.29
unfertilized	2020	45.13	6.43	36.35	0.81	2.17	0.45	7304.06	1.15	0.05	0.21	521.34
unfertilized	2020	45.13	6.43	31.30	0.75	1.83	0.55	7258.74	1.14	0.06	0.22	485.37
unfertilized	2020	45.13	6.43	36.20	0.69	1.66	0.54	9995.68	1.57	0.05	0.19	579.89
NPKCa+m+s	2021	214.76	118.50	77.80	1.75	10.27	2.55	14484.83	2.28	0.26	0.22	1049.38
NPKCa+m+s	2021	214.76	118.50	79.30	1.87	9.87	2.50	15203.74	2.39	0.25	0.22	1085.41
NPKCa+m+s	2021	214.76	118.50	77.10	1.76	11.45	2.49	16743.00	2.63	0.25	0.22	1189.90
NPKCa+m+s	2021	214.76	118.50	79.40	1.89	9.74	3.74	17715.20	2.78	0.37	0.24	1398.63
NPKCa	2021	87.17	53.33	75.30	1.66	9.28	4.24	7201.16	1.13	0.42	0.25	725.44
NPKCa	2021	87.17	53.33	73.20	1.43	8.56	1.31	4960.11	0.78	0.13	0.23	368.32
NPKCa	2021	87.17	53.33	72.40	1.23	7.35	2.35	7907.34	1.24	0.24	0.25	701.51
NPKCa	2021	87.17	53.33	74.90	1.08	6.87	1.41	6455.69	1.01	0.14	0.25	490.21
_PKCa	2021	98.70	53.31	49.80	0.31	1.91	0.93	5153.55	0.81	0.09	0.23	381.11
_PKCa	2021	98.70	53.31	51.70	0.32	1.90	1.02	4340.63	0.68	0.10	0.23	320.82
_PKCa	2021	98.70	53.31	52.40	0.30	1.88	0.83	4651.85	0.73	0.08	0.22	323.82
_PKCa	2021	98.70	53.31	50.90	0.34	2.21	0.66	5003.70	0.79	0.07	0.23	381.67
N_KCa	2021	75.14	15.46	72.60	1.14	8.00	2.75	9550.79	1.50	0.27	0.22	787.94
N_KCa	2021	75.14	15.46	74.90	1.41	7.85	2.17	11288.35	1.77	0.22	0.24	867.37
N_KCa	2021	75.14	15.46	73.00	1.34	8.08	2.22	10256.57	1.61	0.22	0.26	875.74
N_KCa	2021	75.14	15.46	72.30	1.38	8.86	1.90	12587.05	1.98	0.19	0.23	950.68
NP_Ca	2021	35.40	41.15	77.00	1.63	11.49	3.35	12280.50	1.93	0.34	0.25	1045.74
NP_Ca	2021	35.40	41.15	76.10	1.71	11.82	3.27	14997.70	2.36	0.33	0.25	1258.49
NP_Ca	2021	35.40	41.15	73.40	1.72	12.90	2.62	14454.45	2.27	0.26	0.24	1147.46
NP_Ca	2021	35.40	41.15	74.40	1.51	11.36	3.45	17064.27	2.68	0.35	0.24	1374.16
NPK_	2021	75.25	35.41	74.20	1.44	9.86	3.61	11656.91	1.83	0.36	0.26	1129.29
NPK_	2021	75.25	35.41	74.40	1.37	9.21	4.27	11191.81	1.76	0.43	0.25	1042.21
NPK_	2021	75.25	35.41	74.60	1.63	10.15	2.67	9699.69	1.52	0.27	0.26	862.22
NPK_	2021	75.25	35.41	76.40	1.54	11.20	3.45	11593.73	1.82	0.35	0.24	1000.84
unfertilized	2021	40.55	17.58	50.90	0.23	1.42	1.89	4308.29	0.68	0.19	0.28	446.03
unfertilized	2021	40.55	17.58	47.70	0.15	1.05	0.92	3830.09	0.60	0.09	0.23	301.61
unfertilized	2021	40.55	17.58	52.60	0.21	1.15	2.17	3580.38	0.56	0.22	0.24	392.29
unfertilized	2021	40.55	17.58	44.70	0.25	1.57	2.10	4768.07	0.75	0.21	0.27	450.90

Data used for Pearson Correlation test: Part IV

treatment	year	r_s	rL_sB	length_top	biomass_top	rld_top	rmd_top	length_sub	biomass_sub	rld_sub	rmd_sub	SRL	SLA
NPKCa+m+s	2020	1.10	107.77	1304.06	0.22	0.68	0.07	131.92	0.01	0.05	0.00	97.69	12.70
NPKCa+m+s	2020	0.88	125.72	1773.64	0.21	0.93	0.07	306.62	0.02	0.12	0.01	138.85	12.47
NPKCa+m+s	2020	1.50	156.98	2148.32	0.32	1.12	0.11	383.57	0.06	0.15	0.02	103.13	12.94
NPKCa+m+s	2020	0.84	131.04	1805.02	0.16	0.94	0.05	378.72	0.06	0.15	0.01	158.24	12.66
NPKCa	2020	0.89	166.78	2114.05	0.16	1.11	0.06	161.39	0.03	0.06	0.01	175.43	10.24
NPKCa	2020	0.97	106.99	2042.29	0.26	1.07	0.09	55.17	0.04	0.02	0.01	109.70	11.36
NPKCa	2020	0.61	159.91	1778.94	0.11	0.93	0.04	213.31	0.01	0.09	0.00	230.88	12.80
NPKCa	2020	1.25	152.30	1544.56	0.14	0.81	0.05	238.15	0.09	0.10	0.02	117.42	12.43
_PKCa	2020	1.19	178.02	2041.25	0.22	1.07	0.07	56.06	0.00	0.02	0.00	143.65	13.14
_PKCa	2020	1.56	226.33	2110.17	0.22	1.10	0.07	109.67	0.02	0.05	0.01	140.94	12.39
_PKCa	2020	0.43	63.03	571.44	0.06	0.30	0.02	85.36	0.01	0.04	0.00	140.01	13.06
_PKCa	2020	1.31	71.47	593.36	0.16	0.31	0.06	108.02	0.04	0.04	0.01	51.76	12.64
N_KCa	2020	0.43	31.81	330.16	0.08	0.17	0.02	45.93	0.00	0.02	0.00	72.32	11.97
N_KCa	2020	0.35	24.31	185.59	0.03	0.10	0.01	78.90	0.03	0.03	0.01	72.48	11.97
N_KCa	2020	0.17	16.30	126.03	0.03	0.07	0.01	61.64	0.00	0.03	0.00	68.05	12.42
N_KCa	2020	0.91	87.38	1010.20	0.11	0.53	0.03	29.01	0.06	0.01	0.01	110.90	12.25
NP_Ca	2020	0.51	55.04	349.21	0.05	0.18	0.02	130.35	0.02	0.06	0.01	110.24	12.36
NP_Ca	2020	1.03	47.34	246.27	0.07	0.13	0.02	132.13	0.06	0.05	0.02	44.81	12.30
NP_Ca	2020	0.75	123.52	1503.49	0.15	0.79	0.05	72.60	0.00	0.03	0.00	152.62	12.59
NP_Ca	2020	0.88	91.14	800.45	0.12	0.42	0.04	123.02	0.02	0.05	0.01	100.38	12.55
NPK_	2020	1.38	182.38	1754.84	0.19	0.92	0.06	268.16	0.05	0.11	0.01	133.09	11.96
NPK_	2020	1.55	295.20	3015.94	0.25	1.58	0.08	126.38	0.01	0.05	0.00	186.49	12.23
NPK_	2020	0.95	195.73	1872.37	0.15	0.98	0.05	231.87	0.01	0.09	0.00	207.31	12.01
NPK_	2020	0.50	155.10	1663.90	0.08	0.87	0.03	117.78	0.01	0.05	0.00	280.58	12.23
unfertilized	2020	0.51	75.45	350.74	0.05	0.18	0.02	119.93	0.00	0.05	0.00	134.48	12.51
unfertilized	2020	1.77	283.30	839.55	0.09	0.44	0.03	178.43	0.01	0.07	0.00	169.66	11.35
unfertilized	2020	0.14	170.70	439.92	0.01	0.23	0.01	351.43	0.00	0.14	0.00	476.14	10.70
unfertilized	2020	0.29	179.41	594.69	0.02	0.31	0.01	191.59	0.00	0.08	0.00	436.83	11.14
NPKCa+m+s	2020	0.22	46.85	6861.75	0.41	3.60	0.14	7410.37	0.64	1.66	0.09	213.02	11.98
NPKCa+m+s	2020	0.18	32.59	5277.10	0.55	2.77	0.18	6235.94	0.45	1.40	0.06	180.74	12.22
NPKCa+m+s	2020	0.24	50.22	7039.75	0.48	3.69	0.16	5846.47	0.48	1.31	0.07	210.11	13.37
NPKCa+m+s	2020	0.22	41.15	9156.53	0.69	4.80	0.23	6757.88	0.63	1.52	0.09	189.46	12.55
NPKCa	2020	0.25	41.46	4431.28	0.46	2.32	0.15	5345.59	0.47	1.20	0.07	165.71	11.15
NPKCa	2020	0.18	31.54	4092.44	0.31	2.14	0.10	4837.08	0.47	1.09	0.07	178.59	10.75
NPKCa	2020	0.22	41.58	4749.10	0.33	2.49	0.11	5636.92	0.55	1.27	0.08	185.46	10.90
NPKCa	2020	0.21	33.09	4237.46	0.38	2.22	0.13	7341.36	0.77	1.65	0.11	158.61	10.28
_PKCa	2020	0.24	36.52	3016.87	0.27	1.58	0.09	3341.95	0.38	0.75	0.05	155.09	8.69
_PKCa	2020	0.16	37.78	4725.79	0.28	2.48	0.09	3822.32	0.30	0.86	0.04	231.03	9.18

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Data used for Pearson Correlation test: Part IV (Continued)

treatment	year	r_s	rL_sB	length_top	biomass_top	rld_top	rmd_top	length_sub	biomass_sub	rld_sub	rmd_sub	SRL	SLA
_PKCa	2020	0.14	48.29	6595.84	0.27	3.46	0.09	5036.72	0.25	1.13	0.04	352.50	9.37
_PKCa	2020	0.10	36.75	4986.97	0.17	2.61	0.06	4267.56	0.24	0.96	0.03	355.94	9.24
N_KCa	2020	0.17	27.07	3657.76	0.39	1.92	0.13	4430.19	0.39	0.99	0.06	161.76	11.01
N_KCa	2020	0.25	41.63	6191.36	0.53	3.24	0.18	6758.80	0.71	1.52	0.10	163.93	10.32
N_KCa	2020	0.40	67.35	9518.95	0.75	4.99	0.25	9217.18	1.01	2.07	0.14	167.29	10.75
N_KCa	2020	0.21	45.08	6321.95	0.50	3.31	0.17	9095.16	0.61	2.04	0.09	217.14	10.17
NP_Ca	2020	0.27	64.28	6867.73	0.53	3.60	0.18	6093.88	0.31	1.37	0.04	240.03	12.38
NP_Ca	2020	0.21	38.19	5257.27	0.53	2.75	0.18	6721.54	0.51	1.51	0.07	182.05	11.41
NP_Ca	2020	0.18	40.37	5505.41	0.31	2.88	0.10	6616.01	0.53	1.49	0.08	226.99	10.08
NP_Ca	2020	0.18	36.57	5815.27	0.47	3.05	0.16	5112.93	0.35	1.15	0.05	208.55	10.47
NPK_	2020	0.18	29.95	4861.96	0.60	2.55	0.20	5201.48	0.36	1.17	0.05	164.97	11.31
NPK_	2020	0.16	33.93	4080.83	0.39	2.14	0.13	4039.73	0.22	0.91	0.03	207.69	11.19
NPK_	2020	0.16	41.43	4567.43	0.27	2.39	0.09	8114.12	0.51	1.82	0.07	255.68	11.43
NPK_	2020	0.14	30.17	4174.60	0.26	2.19	0.09	6956.52	0.53	1.56	0.08	219.98	10.50
unfertilized	2020	0.23	54.85	2968.39	0.21	1.56	0.07	3972.87	0.24	0.89	0.03	241.02	9.95
unfertilized	2020	0.21	52.97	3939.49	0.25	2.06	0.08	3364.57	0.20	0.76	0.03	253.61	10.42
unfertilized	2020	0.30	62.18	2263.40	0.18	1.19	0.06	4995.34	0.37	1.12	0.05	207.39	11.42
unfertilized	2020	0.32	94.66	4747.29	0.22	2.49	0.07	5248.38	0.31	1.18	0.04	293.13	11.57
NPKCa+m+s	2021	0.25	22.16	8799.49	1.99	4.61	0.66	5685.34	0.56	1.28	0.08	89.14	10.84
NPKCa+m+s	2021	0.25	24.22	7061.98	1.72	3.70	0.57	8141.75	0.78	1.83	0.11	95.56	11.39
NPKCa+m+s	2021	0.22	22.98	8158.54	1.66	4.27	0.55	8584.46	0.83	1.93	0.12	105.57	9.42
NPKCa+m+s	2021	0.38	28.57	8056.17	2.79	4.22	0.93	9659.03	0.95	2.17	0.14	74.37	12.95
NPKCa	2021	0.46	12.19	4325.39	3.87	2.27	1.29	2875.78	0.38	0.65	0.05	26.67	14.60
NPKCa	2021	0.15	9.11	2718.19	1.09	1.42	0.37	2241.92	0.21	0.50	0.03	59.69	12.25
NPKCa	2021	0.32	16.91	5630.96	2.04	2.95	0.68	2276.38	0.31	0.51	0.04	52.82	12.37
NPKCa	2021	0.21	14.77	3472.92	1.00	1.82	0.33	2982.77	0.41	0.67	0.06	71.97	12.27
_PKCa	2021	0.49	42.35	3218.98	0.68	1.69	0.23	1934.56	0.25	0.43	0.04	86.91	10.13
_PKCa	2021	0.54	35.92	2426.73	0.73	1.27	0.24	1913.90	0.29	0.43	0.04	66.88	8.65
_PKCa	2021	0.44	38.93	2112.34	0.48	1.11	0.16	2539.51	0.35	0.57	0.05	87.94	9.78
_PKCa	2021	0.30	35.56	2381.03	0.35	1.25	0.12	2622.67	0.31	0.59	0.04	118.57	10.16
N_KCa	2021	0.34	18.77	5962.00	2.44	3.12	0.81	3588.79	0.31	0.81	0.04	54.61	10.14
N_KCa	2021	0.28	22.60	5603.40	1.58	2.94	0.53	5684.95	0.59	1.28	0.08	81.56	11.03
N_KCa	2021	0.27	19.96	4510.16	1.64	2.36	0.55	5746.41	0.58	1.29	0.08	72.69	11.34
N_KCa	2021	0.21	22.32	6102.22	1.23	3.20	0.41	6484.83	0.67	1.46	0.10	104.11	10.80
NP_Ca	2021	0.29	16.80	6089.16	2.61	3.19	0.87	6191.33	0.74	1.39	0.11	57.52	9.64
NP_Ca	2021	0.28	19.95	10405.64	2.58	5.45	0.86	4592.07	0.69	1.03	0.10	68.50	8.82
NP_Ca	2021	0.20	17.62	7393.23	1.93	3.87	0.65	7061.22	0.69	1.59	0.10	86.50	7.81
NP_Ca	2021	0.30	23.62	9390.59	2.66	4.92	0.89	7673.68	0.79	1.72	0.11	77.71	6.83

Continued on next page

Data used for Pearson Correlation test: Part IV (Continued)

treatment	year	r_s	rL_sB	length_top	biomass_top	rld_top	rmd_top	length_sub	biomass_sub	rld_sub	rmd_sub	SRL	SLA
NPK_	2021	0.37	18.59	8033.93	3.24	4.21	1.08	3622.99	0.37	0.81	0.05	50.68	7.62
NPK_	2021	0.46	19.10	7271.98	3.87	3.81	1.29	3919.82	0.40	0.88	0.06	41.18	7.62
NPK_	2021	0.26	15.02	4231.66	2.00	2.22	0.67	5468.03	0.67	1.23	0.10	56.99	10.63
NPK_	2021	0.31	16.27	5692.42	2.89	2.98	0.96	5901.31	0.56	1.33	0.08	52.77	7.40
unfertilized	2021	1.33	47.58	3163.38	1.77	1.66	0.59	1144.91	0.12	0.26	0.02	35.75	7.97
unfertilized	2021	0.87	57.40	2856.95	0.82	1.50	0.27	973.14	0.10	0.22	0.01	65.58	9.17
unfertilized	2021	1.88	48.86	2859.04	2.09	1.50	0.70	721.34	0.08	0.16	0.01	25.91	8.37
unfertilized	2021	1.33	47.75	2147.95	1.77	1.13	0.59	2620.12	0.32	0.59	0.05	35.74	9.96

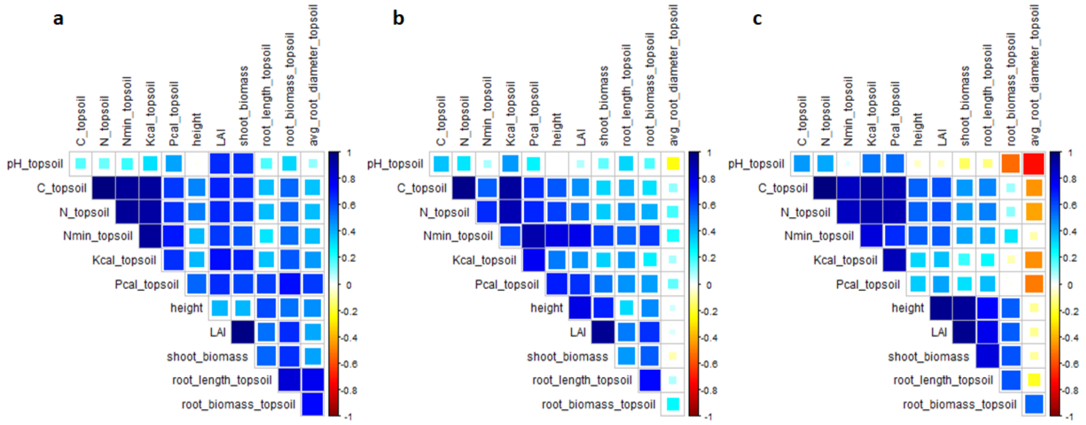


Figure B.8: Pearson correlation for TOPSOIL soil properties, above- and below-ground TOPSOIL traits during the shoot-root sampling dates: (a) First sampling date in growing period 1 (2019/20, BBCH = 23), (b) Second sampling date in growing period 1 (2019/20, BBCH = 43), and (c) First sampling date in growing period 2 (2020/21, BBCH = 69). P-values between –0.3 and 0.3 are not significant.

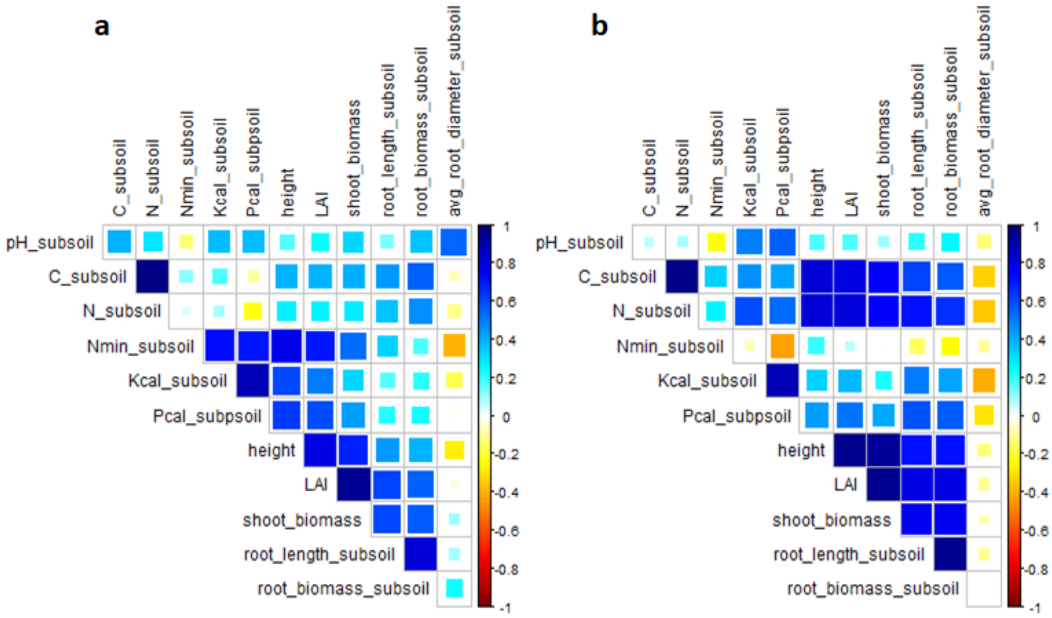


Figure B.9: Pearson correlation for SUBSOIL soil properties, above- and below-ground TOPSOIL traits during the shoot-root sampling dates: (a) Second sampling date in growing period 1 (2019/20, BBCH = 43), and (b) First sampling date in growing period 2 (2020/21, BBCH = 69). P-values between –0.3 and 0.3 are not significant.

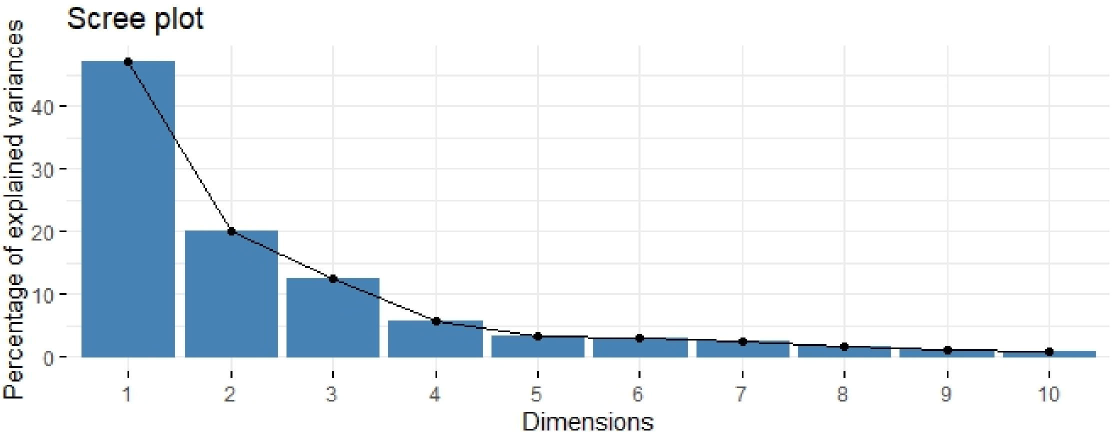


Figure B.10: Scree plot showing the percentage of explained variance for each principal component. The first two components explain the majority of the variance, with subsequent components contributing progressively less.

Appendix C

Supplementary material for chapter 4

Table C.1: The mean values ± standard error of the root:shoot ratio (R:S) and the relative R:S under conventional tillage (CT) and conservation tillage (NT) systems for the three major soil classes and the major soil texture classes. The n is the number of data points per soil class/texture according to the USDA soil texture classification.

Soil	**$\mathbf{R{:}S_{CT}}$**	**$\mathbf{R{:}S_{NT}}$**	**$\mathbf{R{:}S_{CT}}$ / $\mathbf{R{:}S_{NT}}$**	**n**
Major Classes				
Clay	0.14 ± 0.07	0.13 ± 0.04	1.05 ± 0.35	15
Sand	0.18 ± 0.13	0.15 ± 0.08	1.14 ± 0.28	6
Silt/Loam	0.22 ± 0.30	0.27 ± 0.41	0.96 ± 0.32	96
Major Textures				
clay	0.10 ± 0.01	0.12 ± 0.01	0.84 ± 0.03	9
silty clay	0.22 ± 0.03	0.16 ± 0.02	1.38 ± 0.15	6
clay loam	0.10 ± 0.02	0.10 ± 0.02	1.08 ± 0.07	13
silty clay loam	0.05 ± 0.01	0.06 ± 0.01	0.96 ± 0.05	5
sandy clay loam	0.13 ± 0.01	0.15 ± 0.02	0.84 ± 0.04	16
loam	0.29 ± 0.12	0.54 ± 0.28	0.82 ± 0.10	8
silt loam	0.14 ± 0.03	0.19 ± 0.05	1.01 ± 0.06	23
sandy loam	0.65 ± 0.18	0.62 ± 0.18	1.23 ± 0.15	11
loamy sand	0.19	0.13	1.42	1
sand	0.18 ± 0.07	0.15 ± 0.04	1.08 ± 0.12	5
Overall	0.21	0.21	1.07	117

Appendix D

Supplementary material for chapter 5

Key Processes of Process-Based Crop Growth Models

Process-based agroecosystem models (or soil-crop models) are models that represent main processes related to crop development and growth and the interactions with the environment. In the crop growth subroutine of agroecosystem or crop models, biomass production is a function of radiation and temperature. Growth may be further modulated by radiation use efficiency, temperature response curves, as well as water and nutrient stresses (Jamieson et al., 2008).

Crop development

The representation of crop development is commonly made using simplified functions that use a quantitative scale (f.i. from 0 at emergence, to 1 at flowering, and 2 at maturity), the so-called crop development stages (DVS). Crop development mainly depends on air temperature and, in case of winter crops, on day length and vernalization requirements.

Light Interception and Biomass Growth

Photosynthesis enables the production of assimilates available for plant growth using radiation energy. Many common crop growth models are based on the RI-RUE (intercepted radiation RI, radiation use efficiency RUE) concept. The radiation intercepted by the crop canopy over a time interval $[0, t]$ can be calculated using Beer's law (Monsi and Saeki, 1953; Laar et al., 1997) as:

$$RI_t = RAD_t \times \left(1 - e^{-k \times LAI}\right) \tag{S1}$$

where RAD is the global solar radiation (the incident radiation above the canopy), k is the extinction coefficient (-), and LAI is the Leaf Area Index (-). The crop-specific extinction coefficient k depends on the direction of the radiation and on the orientation of the leaves.

Monteith and Moss (1977) established a robust, linear relationship between the accumulated crop biomass and RI. He introduced the concept of RUE as a proxy for the net assimilation rate, which can empirically be estimated as the slope value from the linear regression of accumulated biomass over accumulated RI. The crop- and development-specific RUE is multiplied with RI to estimate the daily increase of biomass. The accumulated dry biomass over a time interval [0, t], (DBM_t) can therefore be written as:

$$DBM_t = \int_0^t RI_t \times RUE_t \times dt \tag{S2}$$

RUE is provided in general as a table in the crop parameter file, but can be scaled by correwction factors e.g. for atmospheric CO2 concentrations and for air temperatures (Savary and Willocquet, 2014). Intercepted radiation increases with LAI, but the rate of increase decreases as LAI increases.

Dry matter partitioning and sink size

Total daily dry matter production is allocated among the various crop organs (leaves, stems, storage organs, and roots) according to partition tables defined as a function of DVS (van Ittersum et al., 2003; Savary and Willocquet, 2014).

$$PARTR_t = Pool_t \times CPR \tag{S3}$$

$$PARTL_t = Pool_t \times CPL_t \times (1 - CPR_t) \tag{S4}$$

$$PARTS_t = Pool_t \times CPS_t \times (1 - CPR_t) \tag{S5}$$

$$PARTSO_t = Pool_t \times CPSO_t \times (1 - CPR_t) \tag{S6}$$

where CPL, CPS, CPR, and CPSO are the partitioning coefficients of assimilates to leaves, stems, roots, and storage organs, respectively, at the development stage at time t. CPL, CPST, and CPSO represent partitioning coefficients relative to the biomass partitioned above ground. CPR is the coefficient of partitioning towards roots, relative to the total plant biomass (Savary and Willocquet, 2014). In general, partitioning towards roots, stems, and leaves occurs until flowering. From this stage onwards, most, if not all, assimilates are allocated to the storage organs. Translocation of stem reserves to the growing storage organs starts at flowering and is simulated by dividing the weight of the stem reserves by a time coefficient (van Ittersum et al., 2003). The direct effect of drought stress on crop growth is expressed as the ratio between actual and potential transpiration and depends on the water content within the rooted soil profile at time t.

RUE correction factors for temperature and atmospheric CO_2 concentrations

Often process-based crop models contain so-called CO_2 response curves. To account for increasing biomass in case of enhanced CO_2 concentrations, crop-specific tables provide correction factors for RUE as a function of atmospheric CO_2 concentration. The effect of CO_2 on the relative radiation use efficiency are often simulated by an exponential relationship (Stockle et al., 1992). Besides, correction factors of RUE as function of mean daytime temperature and low minimum temperature are implemented to allow for a reduction of RUE in case of heat or very low temperatures.

Root growth

A number of 1-D models have been developed that simulate root growth in a multiple layer soil profile. The daily root biomass increase per layer is based on assimilates from the shoot. The daily root elongation is converted into assimilate demand by applying the specific root weight which is a crop-specific and user-defined model parameter. The daily demand of assimilates is limited to the crop-specific maximum elongation rate per day.

Root growth is commonly day-degree dependent and can be restricted below a minimum soil temperature. The root growth begins at germination or at sowing and stops when it reaches either a maximum soil depth (often user defined and crop specific) or when reaching a specific developmental stage, typically flowering. Some models also limit root growth due to some physical or chemical soil properties such as soil layer with high bulk density.

In 1-D crop models, rooting depth is commonly treated separately from root growth in density (root length density). The advancement of the root front (maximal rooting depth of a day) is generally based on degree-days and the root density assumption commonly relies on an exponential decrease of roots with depth (Gerwitz and Page, 1974). Roots start to decay after a user-defined development stage has occurred which is, e.g. in case of cereals, after anthesis or harvest.

Effects of tillage on soil and crop biomass

Maharjan et al. (2018) reviewed approaches to simulate the impact of tillage on soil physical properties and on vertical distribution of organic matter and nutrients implemented in 16 different agro-ecosystem models. The review showed that some models simulate tillage effects on soil bulk density, soil settlement, soil texture redistribution, and several soil hydraulic properties. Most models simulate the incorporation or/and redistribution of organic matter, residues or/and nutrients in the soil, and some models simulate changes in soil porosity and/or soil aggregation (Maharjan et al., 2018). Thus, crop growth is indirectly affected by tillage practices due to changes in soil properties.

Details on the experimental data used for model calibration

The experimental data were taken from a field trial conducted at the agricultural research station Campus Klein-Altendorf of the University of Bonn, situated in the western Germany at 50°37 N, 6°59 E, and 176 m altitude. The trial was conducted with four replicates. The soil texture from 0 to 100 cm depth was 7.2% sand, 69.0% silt, and 23.8% clay. Climatic data were recorded at the research site by the north weather station (http://www.wetter.cka.uni-bonn.de/). Average temperature from August 1st, 2020 to August 31st, 2021, was 11.2 °C, and total precipitation during the same period was 798 mm. Before sowing, soil moisture content was measured using the FDR moisture sensor HH2, which was incorporated into the ML3 Theta Probe 200 (ecoTech Umwelt-Meßsysteme GmbH, Bonn, Germany) at depths of 30, 60, and 90 cm. Winter wheat (*Triticum aestivum*) cultivar cv. Milaneco was sown on August 29th, 2020, with a density of 340 seeds per m^2 and harvested on August 8th, 2021, after 283 days. N fertilizer was applied on March 24th, April 20th and June 7th, 2021, with 50 kg N ha^{-1} applied in the first two dates and 40 kg N ha^{-1} in the last date. The shoot data used for the current study included leaf area index (LAI) collected four times using a LI-3100C Area Meter (LI-COR Biosciences GmbH, Bad Homburg, Germany), shoot biomass measured five times, and straw and grain yield at harvest. To calculate dry biomass, shoot biomass was oven-dried at 60 °C until constant weight and weighed.

During the winter wheat growing season the plant roots were sampled on May 19th, 2021 using a root auger with an inner diameter of 9 cm and a length of 1 m. Soil cores were divided in 10 cm segments and placed into plastic bags. The bags were refrigerated and the soil samples with winter wheat roots were processed sequentially. To extract the roots from the soil, the samples were soaked in tap water and hand-washed using sieves with mesh sizes of 1, 0.83, and 0.5 mm to eliminate the coarse soil. The roots were sorted using tweezers to remove small particles and dead roots. Cleaned roots were stored in tap water at 3 °C until scanning. Afterwards, roots were scanned using an EPSON scanner (HP Expression 1100XL). For this step, the roots of each sample were arranged in an acrylic glass platter and filled with tap water. The scanned images were then analyzed using WinRHIZO software (version Pro 2020a, Regent Instruments, Quebec, Canada) to acquire the root length and root length density data. Last, the roots were dried at 60 °C and weighed to estimate the biomass per layer.

Specific equations of the crop models applied in the modeling exercise

In the modelling exercise performed, the process-based soil-crop models STICS, SIMPLACE, AgroC, and MONICA were calibrated using a simple one-year experimental dataset of winter wheat conducted in Western Germany. Model scenario runs (defined by change in of CO_2, precipitation, N deficiency, tillage depth, or soil bulk density compared to the baseline experiment which are the observed field conditions) were conducted with these five models and the simulated root:shoot biomass ratios were calculated. Specific equations of these models that affect the root:shoot ratio will be outlined in the following section.

SIMPLACE

Lintul 5 (Van Oijen and Lefelaar, 2008) implemented in the model platform SIMPLACE (Enders et al., 2023) was selected for this simulation exercise. Lintul5 has implemented RUE correction factors for temperature and atmospheric CO_2 concentrations (see Supplement). Lintul5 considers the effects of drought and N stress on root:shoot partitioning. In case of drought stress, the fraction of biomass transferred to the root (FRT) is increased by multiplication with the root fraction modification factor (FRTMOD) which is calculated according to:

$$FRTMOD = \max\left(\frac{1.1}{TRANRF} + 0.5\right) \tag{S7}$$

where TRANRF is the transpiration reduction factor calculated by dividing the actual crop transpiration by the potential crop transpiration (and potentially considering a crop-specific drought tolerance factor). FTR ranges between 0 and 1 and FRTMOD is equal or greater than 1 (both factors are dimensionless). The root partition fraction provided in the partitioning table is then multiplied with FRTMOD, thereby increasing the amount of assimilates transferred to the roots in the event of moderate to severe drought stress (water stress factor TRANRF < 0.5). The other fractions are then reduced equally to ensure that the sum of all fractions remains equal to 1. In case of N deficiency, the fraction of biomass transferred to the leaves is reduced with the leaf fraction modification factor (FLVMOD):

$$FLVMOD = e^{-PartitionNStressReduction \times (1-NNI)} \tag{S8}$$

where FLVMOD is the leaf fraction partitioning factor (0,1) and NNI is the Nitrogen Nutrition Index calculated by another model component. The *PartitionNStressReduction* factor is crop specific and user defined. All factors are dimensionless ranging between 0 and 1. The excess biomass is allocated to the stem. The root model SlimRoots implemented in SIMPLACE also comprises a routine to accounts for soil macropores effects on the daily vertical root elongation (Williams and Izaurralde, 2005; Gaiser et al., 2013). To account for the soil strength per soil layer, two approaches have been implemented in the root model SlimRoots. A factor calculated by each of the two approaches reduces the demand for assimilates by the seminal roots when soil bulk density increases, and thus, restricts the daily vertical root elongation rate. However, the presence of macropores in a soil layer can counteract the effect of a compacted soil layer. The SlimWatewr soil water dynamics model applied in this study is a routine for transient simulations of soil water balance of a multiple layer soil profile (Addiscott et al., 1986). Further details on SIMPLACE and the presented components are provided at `https://simplace.net/doc/simplace_modules/`.

STICS

STICS v10 was used with the true root density and continuous trophic link options in this simulation exercise (Beaudoin et al., 2023). Root length growth (RLGJ) depends on the daily production of shoot biomass (DLTAMS), the specific root length/root mass ratio (LONGSPERACP) and the dynamic partition coefficient between below-ground and total biomass (REPRAC):

$$RLGJ(t) = \frac{REPRAC(t)}{1 - REPRAC(t)} \times DLTAMS(t) \times LONGSPERAC_p(t) \times 10^{-2} \tag{S9}$$

REPRAC depends on root development through the normalized root development unit (URAC) (Baret et al., 1992), which is equal to the leaf area index development unit (ULAI) and on specific parameters such as the minimum (MINP), maximum (MAXP) root biomass relative to total biomass and a specific parameter affecting the evolution of the root:shoot ratio (PERM):

$$REPRAC(t) = (MAX_P - MIN_P)\, e^{-ERM\cdot(URAC(t)-1)} + MIN_P \tag{S10}$$

Root:shoot ratio is very temperature-dependent, as URAC is related to the temperature-dependent development of the leaves. The colder the temperature, the higher the REPRAC and ultimately the root:shoot ratio. The trophic effect can be combined with the effects of soil water limitation and mineral nitrogen, but this effect is deactivated for winter wheat in STICS. The influence of bulk density on root growth was adapted on STICS from the formalism proposed by Stockle et al. (1992) and validated by Rebière (1996). Root penetration is unrestricted within the bulk density range delineated by a bulk density under which root growth is reduced due to a lack of cohesion

(DACOHESG) and a bulk density below that the root growth is not limited (DASEUILBASG). Once bulk density surpasses the threshold DASEUILHAUTG, its impact on root penetration remains constant, reflecting the plant's sensitivity to penetration constraints. The effect of ambient CO_2 on the relative radiation use efficiency is simulated by an exponential relationship (Stockle et al., 1992). Further details on STICS and the presented formalisms are described in Beaudoin et al. (2023) and provided at `https://stics.inrae.fr/ressources/documentation`.

AgroC

In AgroC (Klosterhalfen et al., 2017), the root:shoot ratio is predefined in a table (DVS against fraction of dry matter allocated to the shoot (FSH)) and depends on actual development stage (DVS). There are no additional external factors such as temperature or water or nutrient stress altering the partitioning between root and shoot as listed in FSH. Therefore, mainly temperature will alter the root:shoot ratio at given time t as temperature is the main driver for crop phenology (DVS).

In AgroC the daily or hourly glucose assimilation rate G_{phot} (kg CH_2O $[L]^{-2}$ $[T]^{-1}$) is partitioned in dependence of the DVS into the fraction for the shoot and for the root system to build up biomass. According to the labelling experiments performed by Swinnen et al. (1995) for winter wheat, 18.2% of the net assimilation are transferred to the roots, 7.1% are used to build up root biomass, and 5.3% are released as young photosynthetate rhizodeposition. In relation to the amount transferred to the roots this translates into relative fractions of 0.39 and 0.29 for root biomass and exudates, respectively. The relative root exudation fraction f_{exu} (-) thus equals 0.43 (= 0.29 / (0.39 + 0.29)) for winter wheat. In AgroC the root exudation rate R_{texu} (kg C $[L]^{-2}$ $[T]^{-1}$) is computed according to the above-mentioned constant partitioning factor from the dry matter (DM) root growth rate (kg DM $[L]^{-2}$ $[T]^{-1}$):

$$R_{texu} = \Delta W \times f_{rt} \times f_{exu} \times 0.467 \tag{S11}$$

where f_{rt} is the dimensionless partitioning coefficient for roots, and 0.467 kg C kg^{-1} DM is the root-specific dry matter carbon content (Laar et al., 1997). This way, the root exudation shows diurnal variations in the simulations due to the assimilation rate as suggested by, e.g., Hopkins et al. (2013) and Kuzyakov (2006). Additionally, AgroC is the only model applied in this study that uses the Richards equation for soil water dynamic calculations, whereas the other models use so-called tipping bucket models mainly parameterized by field capacity and wilting point as inputs.

MONICA

The MONICA (Model for Nitrogen and Carbon Simulation, `https://gitlab.com/zalf-rpm/monica-docs`) model is a process-based model for simulating plant growth, water and nitrogen dynamics. The model has been applied for simulating crops (Nendel et al., 2011) and grasses (Kamali et al., 2022) in Central Europe. The crop growth concept of MONICA is based on the calculation of assimilate production from radiation at different development stages. MONICA estimates photosynthesis using a set of algorithms presented by Mitchell et al. (1995) which is based on Farquhar and von Caemmerer (1982). The transition from one growth stage to another is driven by the accumulation of temperature sum above a base temperature. The assimilation carbohydrates will be distributed between different crops (in this paper, root, leaf, shoot and grain) and will be converted into above and below-ground biomass. The root:shoot ratio will be then calculated by dividing below- to above-ground biomass.

The simulation of root growth is based on the model proposed by Pedersen and Lauer (2003). The root dry mass is distributed over the depth according to Gerwitz & Page (1974), whereby the rooting depth increases exponentially with the modified thermal sum.

Crop growth in MONICA is limited by drought and N deficiency. Drought is indicated when potential transpiration increases beyond the amount stored in the soil. The reduction factor for drought stress is calculated by the relation of actual to potential transpiration. Drought stress in the model affects the supply of assimilates produced from photosynthesis if the reduction factor drops below a threshold value which is specific for each crop (here 0.85) and its developmental stages. MONICA does not explicitly consider effects of drought stress on C allocation to organs. But it increases the crop-specific rooting depth under drought stress. To simulate water dynamic, MONICA uses a capacity approach suggested by Wegehenkel (2000). The method defines an empirical, texture-dependent rate coefficient based on which controls water percolation above field capacity.

N deficiency is indicated as soon as the crop's tissue N concentration falls below the critical N concentration. The respective reduction factor results from:

$$N_{stress} = 1 - e^{N_m \cdot \left(5 \cdot \frac{N_{act} - N_m}{N_{crit} - N_m}\right)} \tag{S12}$$

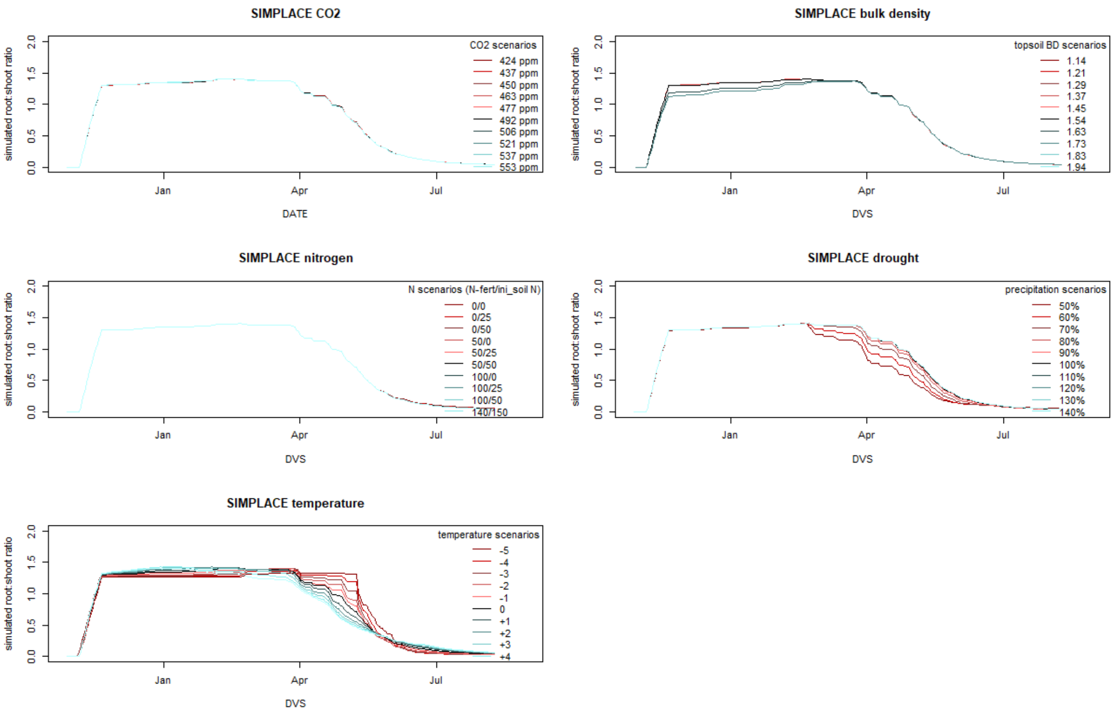
Where N_{stress} is crop reduction factor nitrogen stress, N_{min} is minimum N concentration in the plant tissue, N_{act} is actual nitrogen concentration in the plant tissue and N_{crit} is critical nitrogen concentration in the plant tissue. The root reduction factor is calculated as

$$N_{stress,root} = 1 - \frac{\sqrt{1 - X^2}}{2} \quad \text{where } X = \frac{N_{act,root} - 0.005}{0.005} \tag{S13}$$

Here and in this paper, the response of MONICA to tillage was defined using similar approach presented by SIMPLACE which is based on soil strength and a function of soil bulk density.

Figures

Figures of simulated root:shoot biomass ratios



SIMPLACE CO2

SIMPLACE bulk density

SIMPLACE nitrogen

SIMPLACE drought

SIMPLACE temperature

Figure D.1: Simulated winter wheat root:shoot ratios of the SIMPLACE model (baseline and scenario runs).

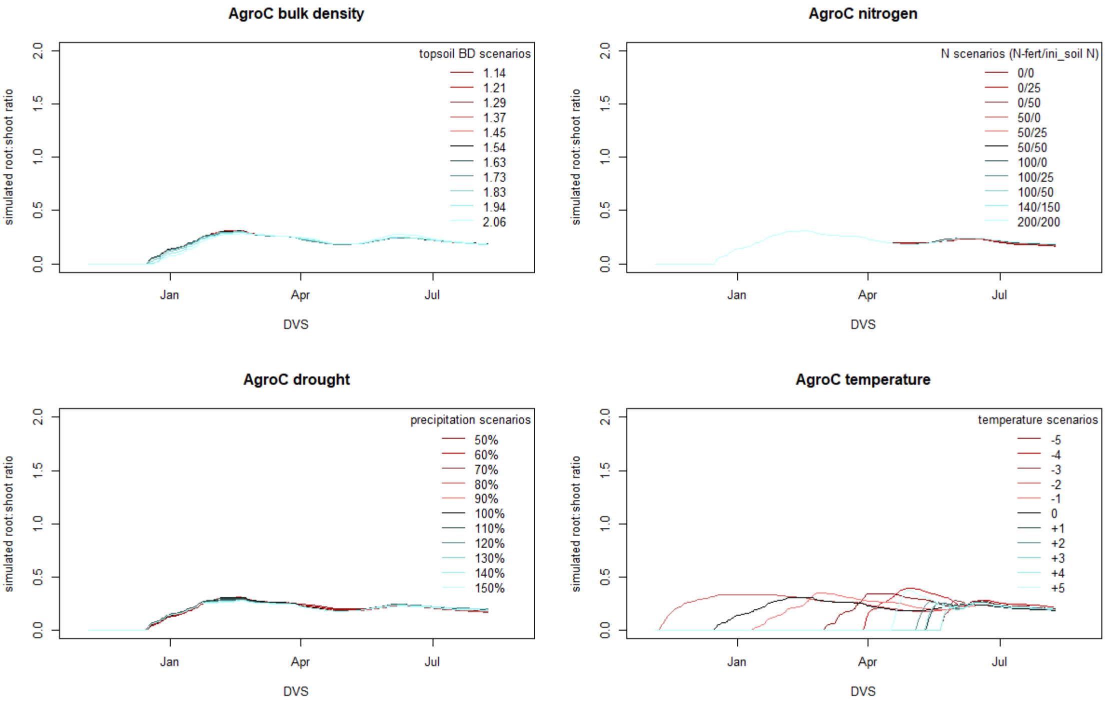


Figure D.2: Simulated winter wheat root:shoot ratios of the AgroC model (baseline and scenario runs).

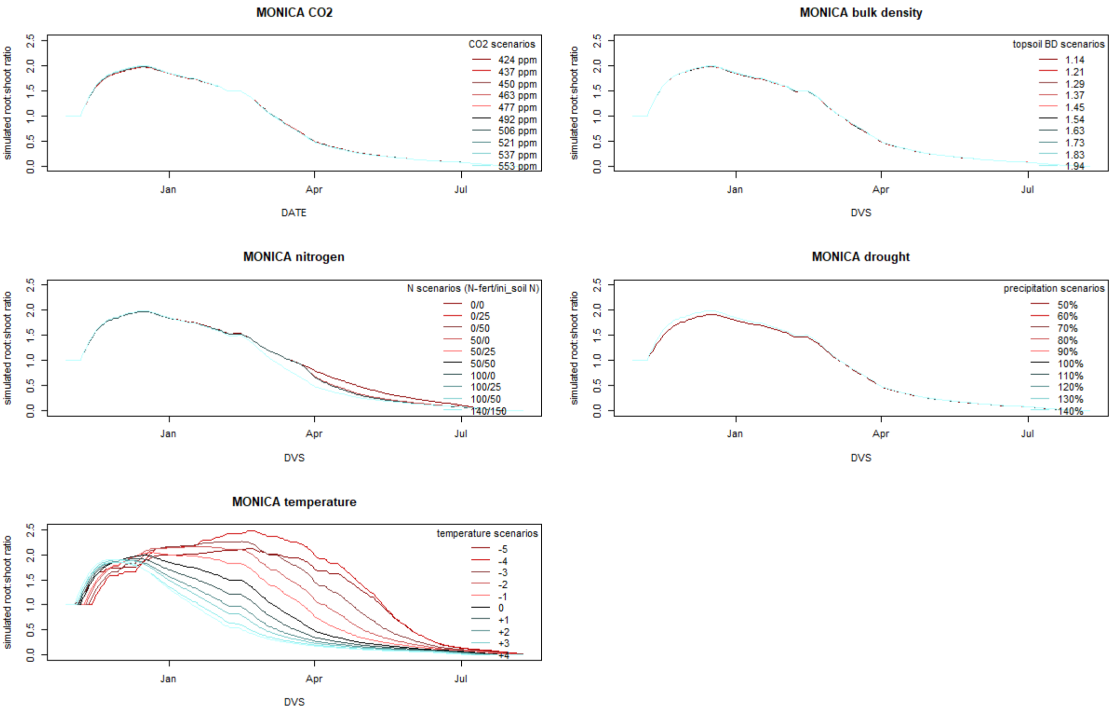


Figure D.3: Simulated winter wheat root:shoot ratios of the MONICA model (baseline and scenario runs).

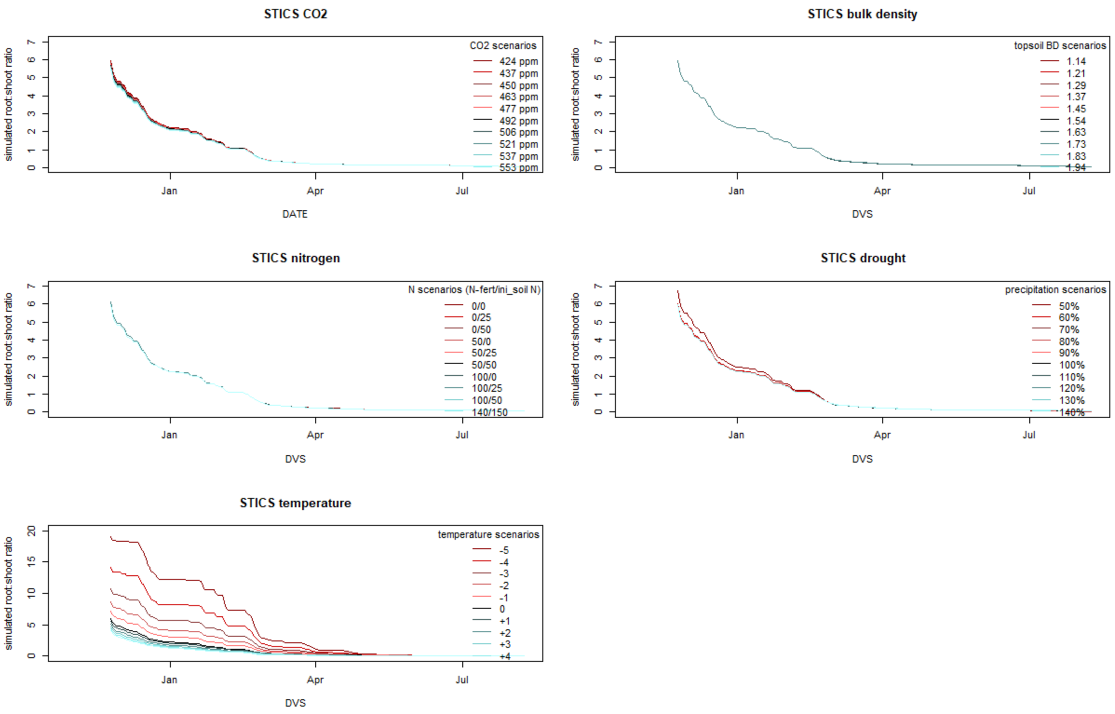


Figure D.4: Simulated winter wheat root:shoot ratios of the STICS model (baseline and scenario runs).

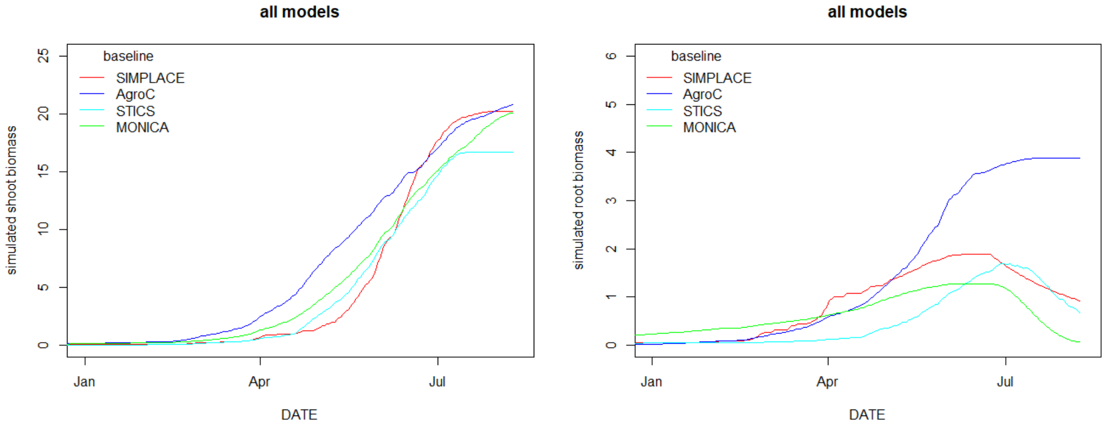


Figure D.5: Simulated winter wheat shoot (left) and root biomass (right) of all models (both as dry matter, in t ha^{-1}) (baseline).

Figures of simulated absolute root biomass

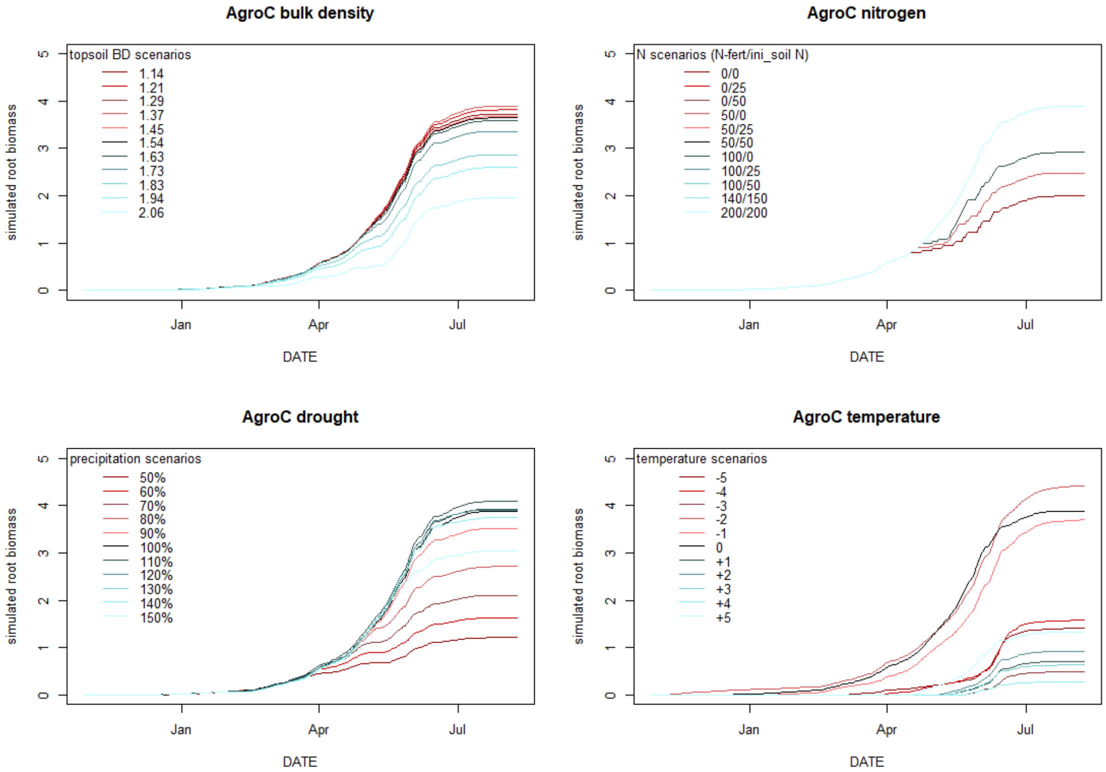


Figure D.6: Simulated winter wheat root biomass (dry matter, in t ha^{-1}) of the AgroC model (baseline and scenario runs).

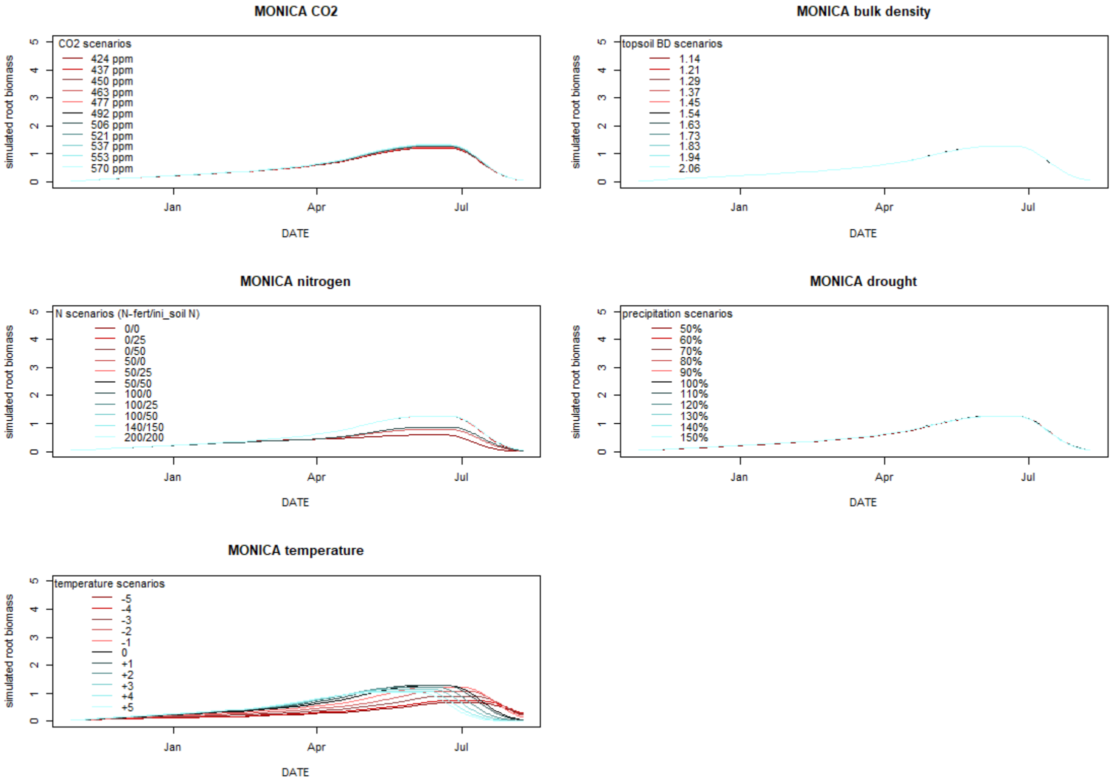


Figure D.7: Simulated winter wheat root biomass (dry matter, in t ha^{-1}) of the MONICA model (baseline and scenario runs).

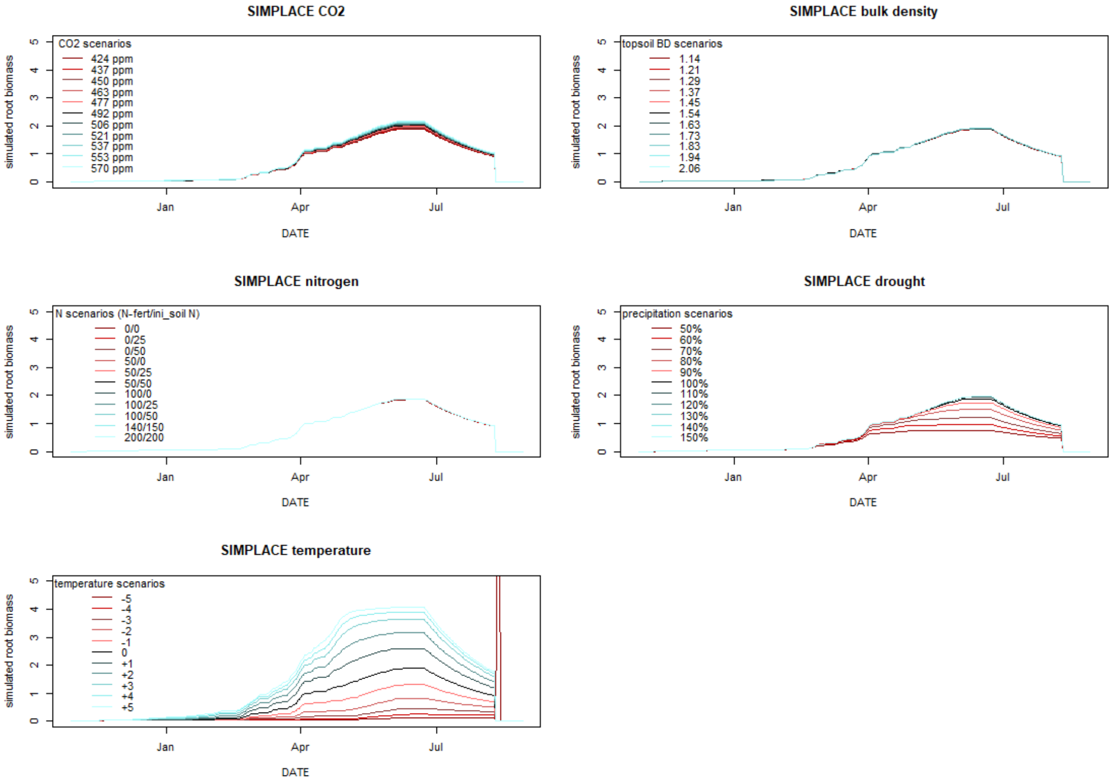


Figure D.8: Simulated winter wheat root biomass (dry matter, in t ha^{-1}) of the SIMPLACE model (baseline and scenario runs).

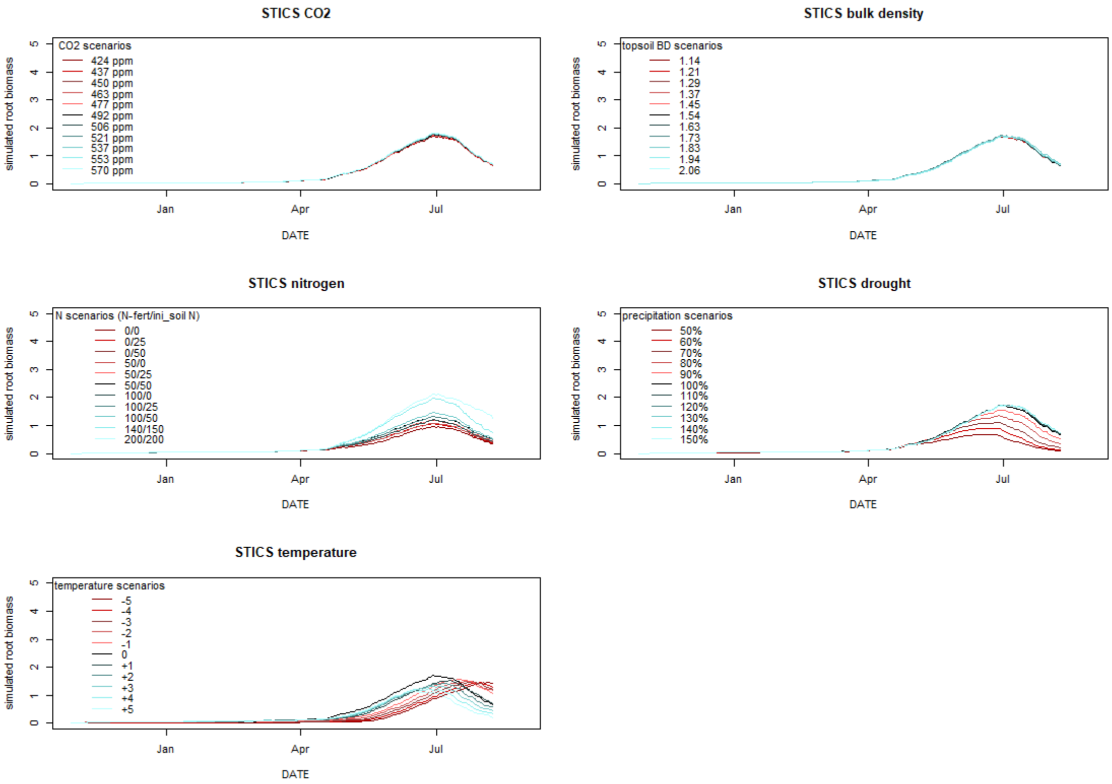


Figure D.9: Simulated winter wheat root biomass (dry matter, in t ha^{-1}) of the STICS model (baseline and scenario runs).

Figures of simulated absolute shoot biomass

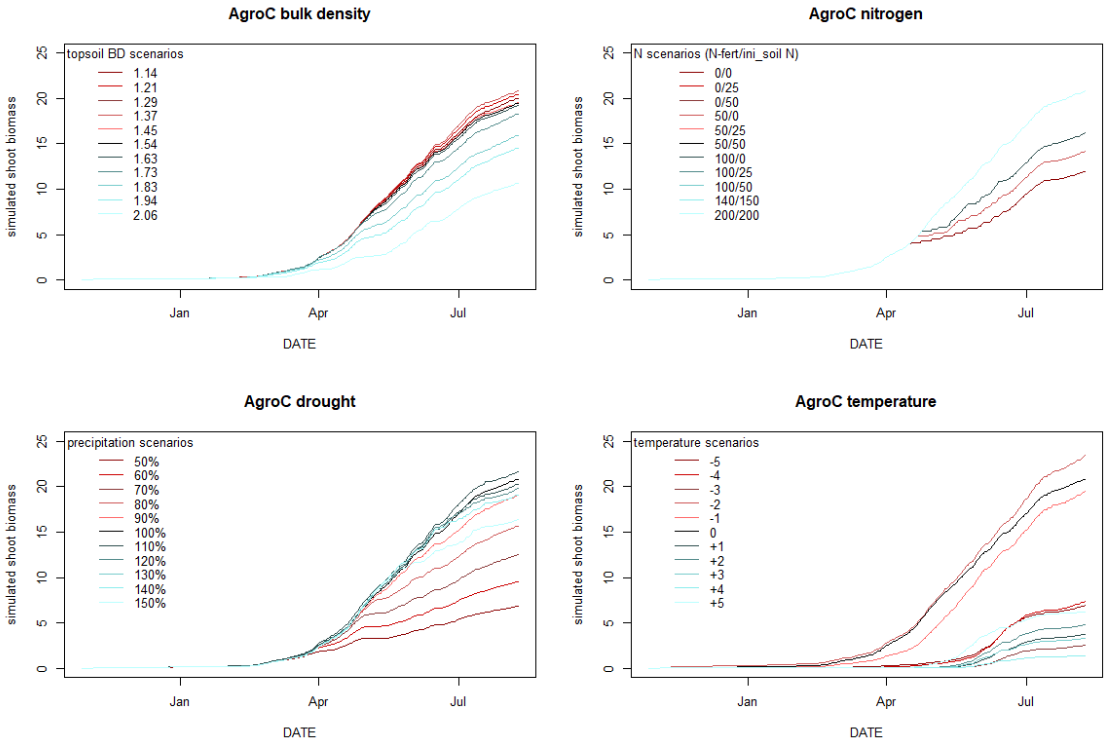


Figure D.10: Simulated winter wheat shoot biomass (dry matter, in t ha^{-1}) of the AgroC model (baseline and scenario runs).

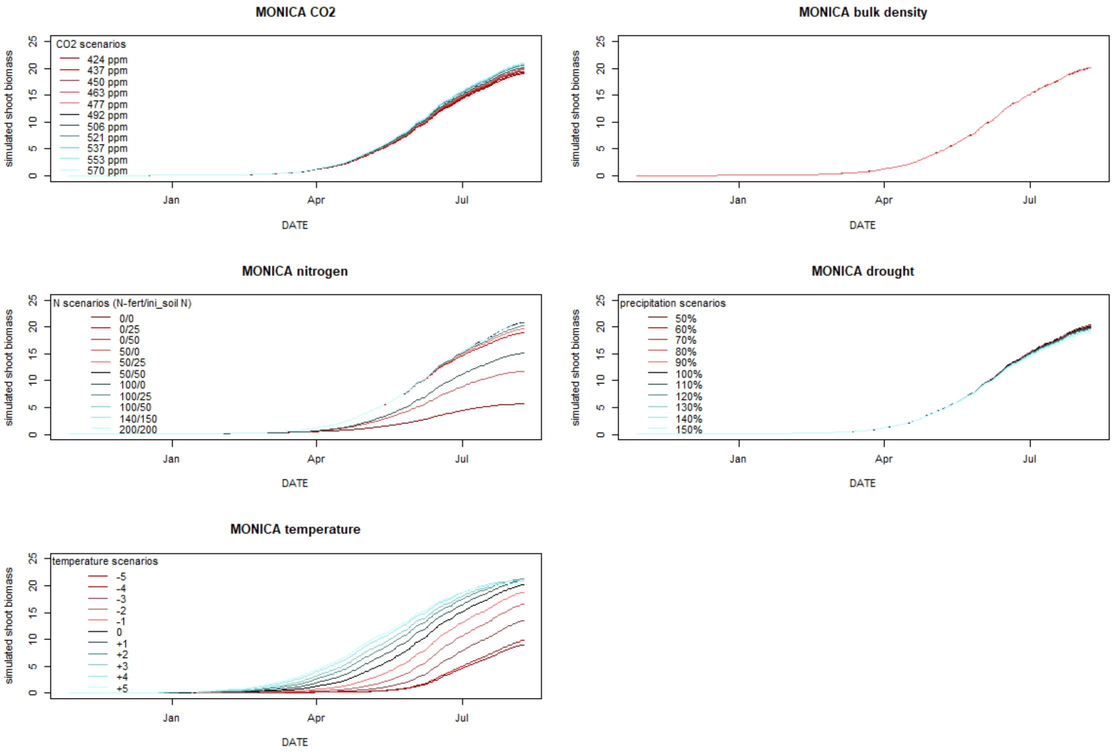


Figure D.11: Simulated winter wheat shoot biomass (dry matter, in t ha^{-1}) of the MONICA model (baseline and scenario runs).

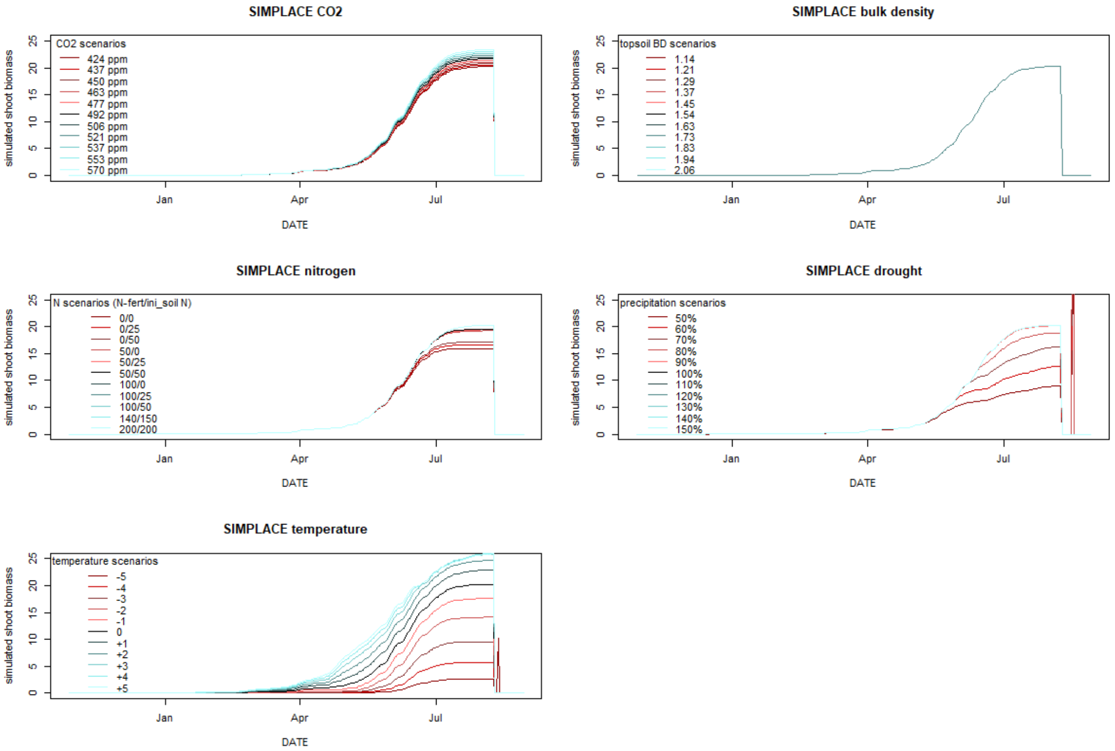
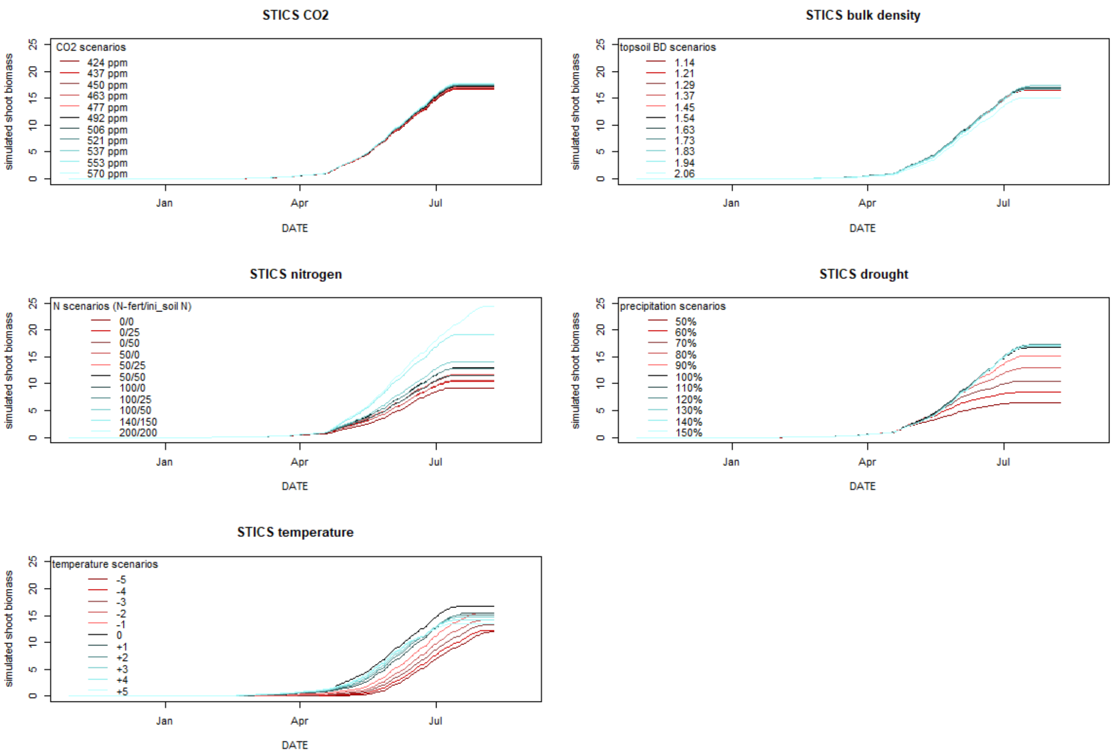


Figure D.12: Simulated winter wheat shoot biomass (dry matter, in t ha^{-1}) of the SIMPLACE model (baseline and scenario runs).



STICS CO2

STICS bulk density

STICS nitrogen

STICS drought

STICS temperature

Figure D.13: Simulated winter wheat shoot biomass (dry matter, in t ha^{-1}) of the STICS model (baseline and scenario runs).

Sources

Table D.1: Summary of studies by factor, author, title, and DOI.

factor	First author and year	title	doi
CO2	Nie et al (2013)	Altered root traits due to elevated CO_2 : a meta-analysis	10.1111/geb.12062
CO2	Vanuytrecht et al (2012)	Quantifying field-scale effects of elevated carbon dioxide concentration on crops	10.3354/cr01096
CO2	Rogers et al. (1996)	Root to shoot ratio of crops as influenced by CO_2	10.1007/bf00017090
CO2	Suter et al (2001)	Elevated CO_2 increases carbon allocation to the roots of *Lolium perenne* under free-air CO_2 enrichment but not in a controlled environment	10.1046/j.1469-8137.2002.00368.x
CO2	Amthor et al. (1994)	Energy content, construction cost and phytomass accumulation of *Glycine max* (L.) Merr. and *Sorghum bicolor* (L.) Moench grown in elevated CO_2 in the field	10.1111/j.1469-8137.1994.tb02990.x
CO2	Franzaring et al 2011	Growth, senescence and water use efficiency of spring oilseed rape (*Brassica napus* L. cv. Mozart) grown in a factorial combination of nitrogen supply and elevated CO_2	10.1016/j.envexpbot.2011.04.003
CO2	Kimball et al 1995	The Effects of Free-Air [CO_2] Enrichment of Cotton, Wheat, and Sorghum	10.1007/3-540-31237-4$_3$
CO2	Wall et al 2006	Interactive Effects of Elevated Carbon Dioxide and Drought on Wheat	10.2134/agronj2004.0089
CO2	Ma et al. (2007)	Availability of soil nitrogen and phosphorus in a typical rice–wheat rotation system under elevated atmospheric [CO_2]	10.1007/s11104-007-9241-5
CO2	Kou et al. (2007)	Effect of elevated atmospheric CO_2 concentration on soil and root respiration in winter wheat by using a respiration partitioning chamber	10.1007/s11104-007-9380-8
CO2	Rønn et al. 2003	Effects of elevated atmospheric CO_2 on protozoan abundance in soil planted with wheat and on decomposition of wheat root	`https://www.jstor.org/stable/24129141`
CO2	Qiao et al. (2010)	Effects of elevated CO_2 concentration on growth and water use efficiency of winter wheat under two soil water regimes	10.1016/j.agwat.2010.06.007

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Table D.1: Summary of studies by factor, author, title, and DOI.

factor	First author and year	title	doi
temperature	Füllner et al. (2012)	Vertical gradient in soil temperature stimulates development and increases biomass accumulation in barley	10.1111/j.1365-3040.2011.02460.x
temperature	Füllner et al. (2012)	Vertical gradient in soil temperature stimulates development and increases biomass accumulation in barley	10.1111/j.1365-3040.2011.02460.x
temperature	Rehman et al. (2019)	Supra-optimal growth temperature exacerbates adverse effects of low Zn supply in wheat	10.1002/jpln.201800654
temperature	Richner et al. (1996)	Shoot-to-Root Relations in Field-Grown Maize Seedlings	10.2134/agronj1996.00021962008800010012x
temperature	Ordóñez et al. (2020)	Root to shoot and carbon to nitrogen ratios of maize and soybean crops in the US Midwest	10.1016/j.eja.2020.126130
temperature	Hou et al. (2018)	Effects of field experimental warming on wheat root distribution under conventional tillage and no-tillage systems	10.1002/ece3.3864
tillage	Haugen-Kozyra et al. (1993)	Nitrogen partitioning and cycling in barley-soil systems under conventional and zero tillage in central Alberta	10.4141/cjss93-021
tillage	House et al. (1984)	Nitrogen cycling in conventional and no-tillage agro-ecosystems: analysis of pathways and processes.	10.2307/2405063
tillage	Trükmann et al. (2008)	Effect of soil compaction on growth of narrow–leafed lupine, oilseed rape and spring barley on sandy loam soil	No DOI is available.
tillage	Chen and Weil (2010)	Penetration of cover crop roots through compacted soils	10.1007/s11104-009-0223-7
tillage	Muñoz-Romero et al. (2012).	The effects of the tillage system on chickpea root growth	10.1016/j.fcr.2011.12.015
tillage	Das et al. (2021)	Conservation tillage and nutrient management practices in summer rice (Oryza sativa L.) favoured root growth and phenotypic plasticity of succeeding winter pea (Pisum sativumL.) under eastern Himalayas, India	10.1016/j.heliyon.2021.e07078
tillage	Guan et al. (2014).	Tillage practices affect biomass and grain yield through regulating root growth, root-bleeding sap and nutrients uptake in summer maize	10.1016/j.fcr.2013.12.015

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Table D.1: Summary of studies by factor, author, title, and DOI.

factor	First author and year	title	doi
tillage	Zhang et al. (2022)	Optimizing planting pattern and nitrogen application rate improves grain yield and water use efficiency for rain-fed spring maize	10.1016/j.still.2022.105385
tillage	Braim et al. (1992)	Effects of simplified cultivation on the growth and yield of spring barley on a sandy soil	10.1016/0167-1987(92)90030-F
tillage	Atwell (1990)	The effect of soil compaction on wheat during early tillering I. Growth, development	10.1111/j.1469-8137.1990.tb00918.x
tillage	Muñoz-Romero et al.	Effect of tillage system on the root growth of spring wheat	10.1007/s11104-009-9983-3
tillage	Barraclough and Weir (1988)	Effects of a compacted subsoil layer on root and shoot growth, water use and nutrient uptake of winter wheat	10.1017/S0021859600081235
tillage	Bian and Cui (2016)	Effects of tillage practices on root characteristics and root lodging resistance of maize	10.1016/j.fcr.2015.10.008
tillage	Wang et al. (2021)	Subsoil tillage promotes root and shoot growth of rapeseed in paddy fields and dryland in Yangtze River Basin soils	10.1016/j.eja.2021.126351
tillage	You et al. (2017)	Short-term effects of tillage and residue on spring maize yield through regulating root-shoot ratio in Northeast China	10.1038/s41598-017-13624-5
tillage	Plaza-Bonilla et al. (2014)	Winter cereal root growth and aboveground–belowground biomass ratios as affected by site and tillage	10.1007/s11104-013-1926-3
tillage	Álvaro-Fuentes et al. (2008)	Management effects on soil carbon dioxide fluxes under semiarid Mediterranean conditions.	10.2136/sssaj2006.0310
tillage	Zhang et al. (2022)	Deep Tillage Improves the Grain Yield and Nitrogen Use Efficiency of Maize (Zea mays L.) Under a Wide–Narrow Row Alternative System in Northeast China	10.1007/s42106-021-00181-1
tillage	Zhou et al. (2012)	Ridge-furrow and plastic-mulching tillage enhances maize–soil interactions: Opportunities and challenges in a semiarid agroecosystem	10.1016/j.fcr.2011.10.010
tillage	Zhouet al. (2016)	A quantitative analysis of root distortion from contrasting wheat cropping systems	10.1007/s11104-016-2836-y

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Table D.1: Summary of studies by factor, author, title, and DOI.

factor	First author and year	title	doi
tillage	Wilhelm (1998)	Dry-matter partitioning and leaf area of winter wheat grown in a long-term fallow tillage comparisons in the US Central Great Plains	10.1016/S0167-1987(98)00154-8
tillage	Gavito et al. (1998)	Early phosphorus nutrition, mycorrhizae development, dry matter partitioning	10.1023/A:1004357322582
tillage	Hou et al. (2018)	Effects of field experimental warming on wheat root distribution under conventional tillage and no- tillage systems	10.1002/ece3.3864
tillage	Piao et al. (2019)	Effects of Soil Tillage and Canopy Optimization on Grain Yield, Root Growth, and Water Use Efficiency of Rainfed Maize in Northeast China	10.3390/agronomy9060336
tillage	Hirte et al. (2021)	Enhanced root carbon allocation through organic farming is restricted to topsoils	10.1016/j.scitotenv.2020.14355
tillage	Piao et al. (2019)	Mulch and no-till impacts on nitrogen and phosphorus leaching in a maize field under sub-tropic monsoon climate	10.1016/j.envc.2021.100346
tillage	Adamič and Leskovše, R. (2021)	Soybean (Glycine max (L.) Merr.) Growth, Yield, and Nodulation in the Early Transition Period from Conventional Tillage to Conservation and No-Tillage Systems	10.3390/agronomy11122477
tillage	Mahata et al. (1992)	Tillage effects on growth and yield of blackgram (Phaseolus mungo) and cowpea (Vigna unguiculata) after wet-season rice on an alluvial sandy clay-loam	10.1016/0378-4290(92)90076-L
N limitation	Welbank et al., 1968	Root growth of a barley crop estimated by sampling with portable powered soil-coring equipment	doi: 10.2307/2401574
N limitation	Anderson, 1988	Tillage and n fertilization effects on maize root growth and root:shoot ratio	doi: 10.1007/BF02375655
N limitation	Barraclough et al., 1989	The effects of prolonged drought and nitrogen fertilizer on root and shoot growth and water uptake by winter wheat	doi: 10.1111/j.1439-037X.1989.tb00778.x
N limitation	Eghball et al., 1993	Root development and nitrogen influx of corn genotypes grown under combined drought and nitrogen stresses	doi: 10.2134/agronj1993.00021962008500010027x

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Table D.1: Summary of studies by factor, author, title, and DOI.

factor	First author and year	title	doi
N limitation	Fang et al., 2022	Root characteristics, utilization of water and nitrogen, and yield of maize under biodegradable film mulching and nitrogen application	doi: 10.1016/j.agwat.2021.107392
N limitation	Feng et al., 2016	Effects of nitrogen application on root length and grain yield of rain-fed maize under different soil types	doi: 10.2134/agronj2015.0367
N limitation	Hadir et al., 2020	Sugar beet shoot and root phenotypic plasticity to nitrogen, phosphorus, potassium and lime omission	doi: 10.3390/agriculture11010021
N limitation	Myers, 1980	The root system of a grain sorghum crop	doi: 10.1016/0378-4290(80)90007-6
N limitation	Otto et al., 2014	The role of nitrogen fertilizers in sugarcane root biomass under field conditions	doi: 10.4236/as.2014.514164
N limitation	Sharifi et al., 2021	Dry matter and nitrogen accumulation and root morphological characteristics of two clonal selections of ‘Russet norkotah’ potato as affected by nitrogen fertilization	doi: 10.1080/01904160500323552
N limitation	Wang et al., 2005	Effects of different irrigation and nitrogen regimes on root growth and its correlation with above-ground plant parts in high-yielding wheat under field conditions	doi: 10.1016/j.fcr.2014.04.011
N limitation	Xue et al., 2014	Effects of nitrogen management on root morphology and zinc translocation from root to shoot of winter wheat in the field	doi: 10.1016/j.fcr.2014.01.009
drought	Zhou et al. (2018)	Drought-induced changes in root biomass largely result from altered root morphological traits: Evidence from a synthesis of global field trials.	10.1111/pce.13356
drought	Kou et al. (2022)	Responses of root system architecture to water stress at multiple levels: A meta-analysis of trials under controlled conditions	10.3389/fpls.2022.1085409
drought	Bacher et al. (2022)	Modifying root-to-shoot ratio improves root water influxes in wheat under drought stress	10.1093/jxb/erab500

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Table D.1: Summary of studies by factor, author, title, and DOI.

factor	First author and year	title	doi
drought	Fang et al. (2017)	Moderate Drought Stress Affected Root Growth and Grain Yield in Old, Modern and Newly Released Cultivars of Winter Wheat	10.3389/fpls.2017.00672
drought	Du et al. (2020)	Effect of drought stress on sugar metabolism in leaves and roots of soybean seedlings	10.1016/j.plaphy.2019.11.003
drought	Pang et al. (2020)	Contrasting responses to drought stress in herbaceous perennial legumes	10.1007/s11104-011-0904-x
drought	Hill et al. (2021)	Morphophysiology of Potato (Solanum tuberosum) in Response to Drought Stress: Paving the Way Forward	10.3389/fpls.2020.597554
drought	Jefferies, 2023	Cultivar responses to water stress in potato: effects of shoot and roots	10.1111/j.1469-8137.1993.tb03761.x