REVIEW ARTICLE

Increasing root biomass derived carbon input to agricultural soils by genotype selection – a review

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Abstract

Background and aims Soil carbon sequestration can play an important role in mitigating climate change. Higher organic C inputs to agricultural soils are needed in order to increase soil organic carbon (SOC) stocks. Genotype selection and breeding towards increased root biomass may enhance root C inputs to the soil and could therefore be a promising, easy-to-implement management option for potentially increasing C sequestration. However, an increase in root C inputs may compromise yield, which is not desirable in terms of food security.

Methods Data from 13 global studies with field experiments were compiled in order to estimate the potential of optimised genotype selection for enhancing root biomass without compromising the yield of winter wheat, spring wheat, silage maize, winter rapeseed and sunflower. A lack of data on the effect of variety on rhizodeposition was identified which thus had to be excluded.

Results Systematic genotype selection increased mean yields by 52% and mean root biomass by 22% across all crops and sites. A median root C increase of 6.7% for spring wheat, 6.8% for winter rapeseed, 12.2% for silage maize, 21.6% for winter wheat and 26.4% for sunflower would be possible without a yield reduction.

Conclusion Overall, this review demonstrates that optimised genotype selection can be a win-win option for increasing root biomass C input to soil while maintaining or even enhancing yield.

Keywords Root biomass · Root carbon inputs · Root to shoot ratio · Climate change mitigation · Carbon sequestration

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Introduction

Soils store more than half of all terrestrial carbon (C) (Jobbagy and Jackson 2000) and can be a sink or source for atmospheric CO_2 (Lal 2004). The accumulation of C in soils could therefore play an important role in mitigating climate change and sustaining agricultural productivity and soil health (Lal 2004). In order to build up soil organic carbon (SOC) stocks in agricultural soils or maintain them with a changing climate, increased organic carbon (OC) inputs are needed (Riggers et al. 2021). Various management

strategies for SOC sequestration have been identified, such as minimising bare fallow periods, adjusting nitrogen (N) fertilisation, increasing the recycling of organic material, and non-harvesting of crop residues (Kätterer et al. 2012; Paustian et al. 2016). However, aboveground biomass is used in many ways, such as for food and fodder, but also as a renewable source of energy or fibre. Thus, there is limited potential for increasing aboveground C inputs to soils without compromising other agricultural targets. In contrast, there is hardly any competing use for most crop roots as they are non-harvestable. This does not apply for crops where the roots are the agricultural product such as sugar beet, carrots and potatoes as their underground storage organs are completely harvested and removed from the field. In agricultural soils, crop roots are the major source of SOC (Poeplau et al. 2021) as root C has a residence time in soils two to three times longer than that of other crop residues or manure-derived C inputs (Kätterer et al. 2011; Menichetti et al. 2015) and is therefore more effective at maintaining and building up SOC. Therefore, enhancing root biomass could introduce additional OC into agricultural soils and thus become an option for potentially sequestering C in soils.

Unfortunately, the quantification of root C inputs in field experiments is labour intensive, and methods vary greatly and are hard to compare (Freschet et al. 2021). Therefore, in soil C modelling, root C inputs are mostly estimated from crop yields using allometric functions (Keel et al. 2017). These allometric functions are specific to crop type and relate the yield to the amount of aboveground and belowground plant biomass, including the root:shoot ratio (Jacobs et al. 2020; Keel et al. 2017). There are no genotype-specific allometric functions due to an absence of data, but the few existing studies suggest varying root:shoot ratios between genotypes. For example, Fang et al. (2017) found a root:shoot ratio of 1.13 in a wheat landrace, while two modern cultivars had root:shoot ratios of 0.61 and 0.81. Thus, genotypic variability is a cause of considerable uncertainty around SOC projections in agriculture. This variability does, however, offer great potential for increasing root biomass C inputs, which is assessed in this study.

It is difficult to reduce these uncertainties and even more challenging to maintain current cropland productivity in light of climate change with increasing extreme weather events (Anderson et al. 2020)

because agricultural production is very site dependent. Higher temperatures may limit root growth, alter root system architecture, and reduce root:shoot ratios (Koevoets et al. 2016). Lynch (2013) suggested introducing a new ideotype of maize roots adapted to climate change, where the deep steep roots would optimise water and nitrogen acquisition.

Optimised genotype selection and breeding towards more roots in general may enhance yield stability under future climatic conditions and be key to successful climate change adaptation by agricultural systems of the future. However, roots have not so far been a focus for breeders, and there is very limited knowledge about the root biomass of different genotypes of various crop types. This review compiled existing studies and experimental data on root biomass, aboveground biomass and the yield of different genotypes of arable crops in order to estimate the potential of genotype selection for enhancing root biomass and thereby root biomass C inputs into agricultural soils. The hypotheses of this review were: (a) genotypes of arable crops differ significantly in root biomass, (b) it is possible to increase root biomass while maintaining yield, and (c) the root:shoot ratio differs significantly between different genotypes of arable crops.

Material and methods

Data collection

To quantify the effects of genotype selection on root biomass C inputs, a literature survey was conducted using the electronic databases Scopus and ISI Web of Science to identify studies that have measured root biomass, aboveground biomass and the yield of different genotypes of important arable crops. This survey focused on the agricultural annual crops of wheat, oilseed rape, maize, barley, rye, sunflower, triticale, potato and sugar beet. The following search terms were used: crop root genotype OR crop root cultivar, with results refined by biomass OR matter in "Article Title, Abstract or Keywords". The results from both databases were merged, and resulted in 1348 studies as an output of the search. In addition, an unpublished dataset from Switzerland was provided by Andreas Hund et al. (not published).

In the present study, it was necessary to depict at least a small population at each site, thus a minimum of four genotypes per study were needed. This led to the identification of 198 studies with a sufficient number of genotypes. Studies that did not provide the necessary information were excluded by the criteria outlined in Supplementary Fig. 1: i) studies where different genotypes of one crop were not grown at the same site, ii) greenhouse trials and experiments with plants grown in pots, and iii) studies where root biomass, shoot biomass and yield were measured before anthesis or were missing. These requirements led to a dataset of 13 studies (see Table 1). No appropriate data for barley, rye, triticale, potato and sugar beet were found. If different water or fertilisation treatments were available in the study, treatment close to agricultural practice was considered to avoid effects caused by water stress or large fertilisation differences.

For data presented graphically, the authors were contacted to provide data or data were extracted using WebPlotDigitizer (Ankit Rohatgi 2021). Furthermore,

Table 1 Overview of the studies included

Code	Location	Crop	MAT (°C) of the sampling year	MAP (mm)	Number of genotypes	Sampling depth (cm)	Author	DOI
BE-Bas BE-Mar BE-Rav	Bassevelde, Belgium Marelbeke, Belgium Ravels, Belgium	Silage maize	18.6	860	8	0–30	Xu et al. 2020	https://doi.org/10.1016/j.eja.2020.126121
CH-Zür	Zürich, Switzerland	Winter wheat	9.7	1463	8	0–20	Hund et al.	Not published
CN-Lis	Lishu, China	Silage maize	6.8	580	8	0–35	Shao et al. 2019	https://doi.org/10.1007/s11104-019-03964-8
DE-Ost	Ostenfeld, Germany	Silage maize	8.9	847	10	0–60	Taube et al. 2020	https://doi.org/10.3389/fpls.2020.01214
FR-Cle	Clermont-Ferrand, France	Winter wheat	10.1	975	16	0–30	Allard et al. 2013	https://doi.org/10.1016/j.eja.2012.12.004
FR-LeR	Le Rheu, France	Winter rape	11.9	737	6	0–100	Vazquez-Carrasquer et al. 2021	https://doi.org/10.3389/fpls.2021.641459
IN-His	Hisar, India	Winter wheat	25.3	509	5	0–100	Tyagi et al. 2004	–
IN-Nas	Nashipur, India	Spring wheat	25.78	1518.4	10	0–10	Jahan et al. 2019	https://doi.org/10.30848/PJB2019-2(11)
IN-Tez	Tezpur, India	Winter wheat	24	740	7	0–30	Baruah et al. 2017	https://doi.org/10.1071/FP17029
IR-Tab	Tabriz, Iran	Winter rape	16	1360	14	0–100	Norouzi et al. 2008	https://doi.org/10.1234/4.2008.1230
MX-Obr	Obregon, Mexico	Spring wheat	24.9	361	10	0–120	Lopes et al. 2011	https://doi.org/10.2135/cropsci2010.07.0445
PK-Fai	Faisalabad, Pakistan	Sunflower	24.8	526	12	0–100	Rauf et al. 2008	https://doi.org/10.1080/09064710701628958
ZA-Kwa	KwaZulu-Natal, South Africa	Winter wheat	18	738	99	0–60	Mathew et al. 2019	https://doi.org/10.1111/jac.12332

data on soil texture, mean annual precipitation (MAP) and mean annual temperature (MAT) were compiled as potential explanatory variables. If there was no information on MAP and MAT, the gaps were filled with data from weatherbase.com, selecting the closest weather station.

Calculations & statistics

Equations developed by Fan et al. (2016) were used to extrapolate root biomass to be able to compare the different studies and sampling depths (see Eq. 1):

$$R_d = R_{d_{obs}} \times \frac{1 + \left(\frac{d}{d_a}\right)^c + \left[1 - \frac{1}{1 + \left(\frac{d_{max}}{d_a}\right)^c}\right] \times d}{1 + \left(\frac{d_{obs}}{d_a}\right)^c + \left[1 - \frac{1}{1 + \left(\frac{d_{max}}{d_a}\right)^c}\right] \times d_{obs}}$$

(1)

where R_d is the root mass for the selected depth d. All root biomass data were harmonised for the depth 100 cm. $R_{d_{obs}}$ is the root mass for the observed depth and d_{max} is the crop-specific maximum rooting depth derived from the literature. d_a, d_{max} and c are the fitted equation parameters for each crop (Fan et al. 2016) (see Table 2).

To harmonise the various studies and make the data comparable, area-related units (Mg ha^{-1}) were calculated. If biomass per plant was assessed in the studies, plant densities were estimated based on available information on seeds m^{-2}, row spacing and germination rate to upscale to area-related units.

Following Bolinder et al. (2007), a root biomass C content of 45% was assumed to calculate total root C, but root exudates were not considered. As the objective of the review was to estimate the potential increase in root biomass C inputs based on variety selection, the maximum and average root

Table 2 Estimated parameters for root biomass calculation from Fan et al. (2016)

Crop	d_a	d_{max}	c
Wheat	17.2	150.4	−1.286
Maize	14.9	118.3	−1.151
Rapeseed	9.9	105.6	−0.473
Sunflower	10.0	133.0	−0.671

biomass observed in a study/population needed to be compared. Thus, it was assumed that the variability between the selected genotypes was representative of the entire population and the data distribution was skewed towards lower biomasses. Thus, the genotype with the median root biomass was identified and the corresponding yield used as the reference for this population:

Potential root C increase = root C_{genotype} − root C_{reference}

(2)

Potential yield increase = yield_{genotype} − yield_{reference}

(3)

To test for differences in the response variables of root biomass and root:shoot ratio, we fitted linear mixed-effects models to the data with lme4 (Bates et al. 2015). As none of the studies had used the same genotypes, the data were perfectly nested and it was not possible to test for differences between genotypes. To test for differences between means of locations or crops, these were modelled as fixed effects. To test for correlations between root biomass and climate variables, for example, location was treated as a random effect to account for different site-specific sources of variance in the root data.

All the calculations were performed with R Studio (R Core Team 2020), R version 4.1.3, using the package Tidyverse (Wickham et al. 2019).

Results

Root biomass

Overall, 13 studies were collected with a total of 212 genotypes of winter wheat, spring wheat, winter rapeseed, silage maize and sunflower under various growing conditions. The median root biomass among all crops was 1.5 Mg ha^{-1} yr^{-1}, while the variation across median per crop ranged from 1.33 to 2.39 Mg ha^{-1} yr^{-1} (Table 3). The variation in root biomass between crops, expressed as the standard deviation, was 0.57 Mg ha^{-1} yr^{-1}, and the mean standard deviation of genotypes within sites within crops was 0.40 Mg ha^{-1} yr^{-1}. Root biomass did not differ significantly between crops in this small dataset.

Among all the sites, winter wheat had a median root biomass of 1.33 Mg ha^{-1} yr^{-1} (CV = 57.21),

Table 3 Variation in root biomass per crop type. CV is the coefficient of variation in per cent. Standard deviation, maximum, median and minimum are given in the unit Mg ha^{-1} yr^{-1}

Crop	Silage maize	Spring wheat	Sunflower	Winter rapeseed	Winter wheat
Standard deviation	0.43	0.47	0.45	0.60	0.92
CV [%]	25.66	31.13	29.22	23.60	57.21
Maximum	2.49	2.87	2.44	3.82	6.56
Median	1.72	1.51	1.46	2.39	1.33
Minimum	0.90	0.67	1.00	1.71	0.76
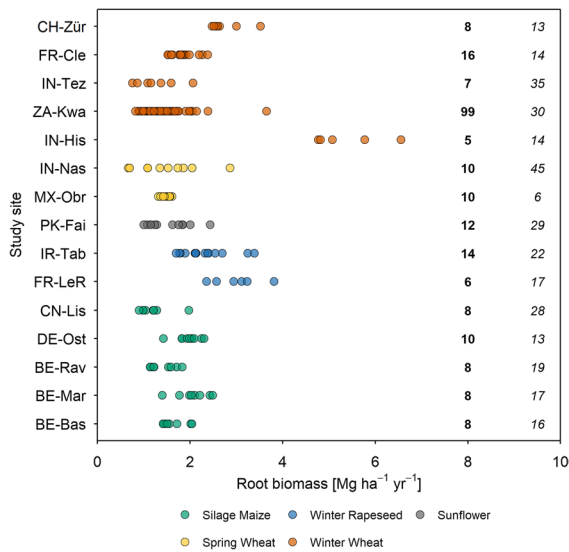
Fig. 1 Belowground biomass of all genotypes of field-grown crop types. The number of genotypes tested at each study site (n) is displayed in bold; the coefficients of variation [%] (CV) are depicted in italics
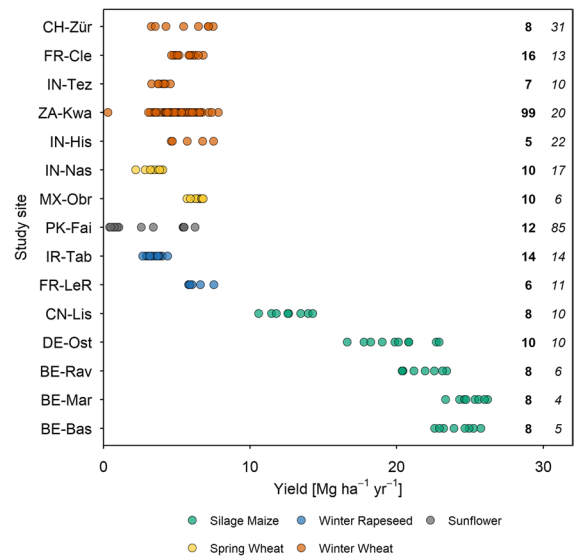

Fig. 2 Yield (total aboveground biomass of silage maize and grain yield of spring wheat, winter wheat, sunflower and winter rapeseed) of all genotypes. The number of genotypes tested at each study site (n) is displayed in bold; the coefficients of variation [%] (CV) are depicted in italics

silage maize had a median root biomass of 1.72 Mg ha^{-1} yr^{-1} (CV = 25.66), and winter rapeseed had the highest median root biomass of all the crops at 2.39 Mg ha^{-1} yr^{-1} (CV = 23.60). The only study on sunflower showed a median root biomass of 1.46 Mg ha^{-1} yr^{-1} (CV = 29.22) (Table 3). The root biomass per genotype is displayed in Fig. 1.

Aboveground biomass

Aboveground biomass had a median value of 10.62 Mg ha^{-1} yr^{-1} and ranged between 2.92 and 26.21 Mg ha^{-1} yr^{-1} among all crops. Aboveground biomass was not correlated with MAT, MAP or clay content (Supplement Table 1). The yield (total aboveground biomass) of silage maize was significantly higher, at 21 ± 5 Mg ha^{-1} yr^{-1}, than the grain yield of

all other crops (p < 0.05). The ranges of total aboveground biomass yield and grain yield per study site are depicted in Fig. 2.

Silage maize showed a median yield of 22.26 Mg ha^{-1} yr^{-1} with a CV of 22.19% (Table 4). The median yield of winter wheat was 5.15 Mg ha^{-1} yr^{-1} (CV = 20.69%) and for spring wheat it was 4.88 Mg ha^{-1} yr^{-1} (CV = 31.98%). Winter rapeseed had a median yield of 3.73 Mg ha^{-1} yr^{-1} (CV = 33.04%). The only study on sunflowers showed a median yield of 1.81 Mg ha^{-1} yr^{-1} (CV = 84.67%).

Sixty-three of the 212 genotypes included in this study showed potential for increasing root biomass C without compromising yield. The potential for increasing root biomass C inputs (Eq. 2) and yield (Eq. 3) did not seem to follow a positive correlation;

Table 4 Variation in yield (total aboveground biomass of silage maize and grain yield of spring wheat, winter wheat, sunflower and winter rapeseed) per crop type. CV is the coefficient of variation in per cent. Standard deviation, maximum, median and minimum are given in the unit Mg ha^{-1} yr^{-1}

Crop	Silage maize	Spring wheat	Sunflower	Winter rapeseed	Winter wheat
Standard deviation	4.58	1.57	2.33	1.43	1.07
CV [%]	22.19	31.98	84.67	33.04	20.69
Maximum	26.21	6.80	6.24	7.54	7.83
Median	22.26	4.88	1.81	3.73	5.15
Minimum	10.58	2.20	0.43	2.68	0.30
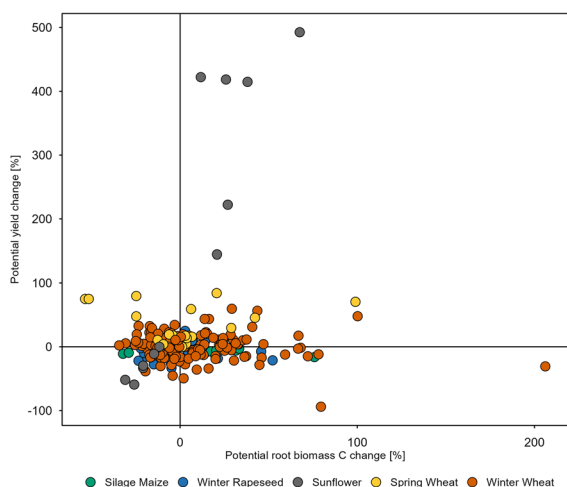
Fig. 3 Relative potential yield and root biomass C change [%] of all field-grown genotypes in comparison with the median root biomass of each study's genotype and its corresponding yield

there appeared to be either a large yield increase or a large root biomass and therefore root biomass C input increase, but not both (Fig. 4).

The greatest potential for increasing root biomass C without compromising yield was observed in winter wheat (0.67 Mg C ha^{-1} yr^{-1}), followed by spring wheat (0.64 Mg C ha^{-1} yr^{-1}). The median potential yield increase varied from 0.34 Mg ha^{-1} yr^{-1}

(winter rapeseed) to 6.63 Mg ha^{-1} yr^{-1} (sunflower). Sunflower also showed the greatest potential for increasing yield (4.43 Mg C ha^{-1} yr^{-1}) (Fig. 3).

Root:shoot ratios

Root:shoot ratios had a median of 0.13, and ranged between 0.05 and 0.80 among all crops. Winter wheat showed a median root:shoot ratio of 0.15 (CV=66.59%), which was the highest median root:shoot ratio of all crops with the highest variation. Winter rapeseed had a similar root:shoot ratio of 0.14, but a lower variability (CV=16.46%). Spring wheat had a median root:shoot ratio of 0.12 (CV=51.38%). Sunflower and silage maize had the lowest median root:shoot ratios (0.09 and 0.08) of all crops, but sunflower showed more variability (CV=58.81%) than silage maize (CV=28.57%). Winter wheat, summer wheat and sunflower seemed to be more flexible than silage maize and winter rapeseed (Table 5, Fig. 4).

Discussion

Can genotype selection increase root biomass C inputs to soil?

The presented data show that there is a great variability in root biomass production between different genotypes

Table 5 Variation of root:shoot ratios per crop type. CV is the coefficient of variation in per cent

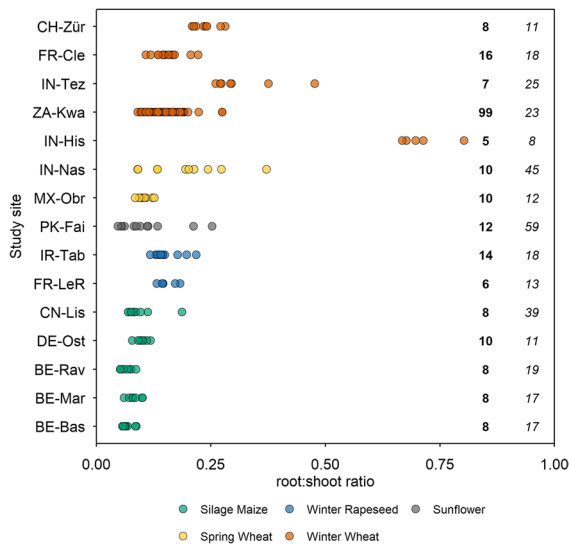| Crop	Silage maize	Spring wheat	Sunflower	Winter rapeseed	Winter wheat
Standard deviation	0.02	0.08	0.06	0.02	0.12
CV [%]	28.57	51.38	58.81	16.46	66.59
Maximum	0.19	0.37	0.25	0.22	0.80
Median	0.08	0.12	0.09	0.14	0.15
Minimum	0.05	0.09	0.05	0.12	0.09

Fig. 4 Root:shoot ratios of all genotypes of field-grown crop types. The number of genotypes tested at each study site (n) is displayed in bold; the coefficients of variation [%] (CV) are depicted in italics

of a given crop, with a factor 1 to 4 between the genotypes with the lowest and highest root biomass at the same site. Therefore, optimised genotype selection can increase root biomass C inputs to the soil by selecting genotypes that grow more root biomass. The C bound in this additional root biomass can in turn contribute to potentially increasing SOC stocks (Kätterer et al. 2012). Breeding efforts in recent decades have resulted in increasing yields (Fischer and Edmeades 2010) by focusing on the water and nutrient uptake of the root system, but not on the size of the root system (van Noordwijk and de Willigen 1987; Kell 2011; Lynch and Wojciechowski 2015). Thus, modern varieties are known to grow fewer roots per plant and have smaller root systems than older varieties (Fradgley et al. 2020; Zhu et al. 2019). This might give the impression that in modern genotypes of common crops it is not feasible to increase root biomass C inputs to agricultural soils. To test this assumption, Taube et al. (2020) recreated a timeline of the breeding progress in silage maize in Germany from 1970 to 2012. It showed that root biomass did not increase significantly as the advances in breeding were being made, even though yield increased by 0.13 t ha^{-1} year^{-1}. Thus, they concluded that newer genotypes are not likely to enhance the C sequestration potential through higher root biomass C inputs. The dataset from this review contradicts this conclusion

because 14 of the 26 silage maize genotypes included in this study showed potential to increase root biomass and therefore root biomass C inputs to agricultural soil by a mean of 0.14 Mg C ha^{-1} yr^{-1} (17.6%). For example, the genotype Ronaldinio showed a higher yield than the median (+ 2.71 Mg ha^{-1} yr^{-1}) and the highest root biomass (+ 0.13 Mg ha^{-1} yr^{-1}) in the study by Taube et al. (2020). Thus, modern genotypes of maize are also able to increase root biomass C inputs to agricultural soils. Due to constant root:shoot ratios in maize, this surplus of root biomass C could be a consequence of the yield progress in silage maize.

Fang et al. (2017) compared three winter wheat genotypes: one landrace and two newer cultivars (released in 2004 and 2014). The landrace produced 34–38% more topsoil root mass and 36–62% less subsoil root biomass under rain-fed conditions than the newer genotypes. Generally, the landrace produced more root biomass (226 g m^{-2} yr^{-1}) under rain-fed conditions than the newer cultivars (170 g m^{-2} yr^{-1} and 203 g m^{-2} yr^{-1}) (Fang et al. 2017). Since only modern genotypes of winter wheat were represented in these data, but root biomass production still differed by 86.4 to 283 g m^{-2} yr^{-1} between the genotype with the lowest and the highest root biomass at the same site, it could be concluded that modern winter wheat genotypes can also increase OC inputs to soils.

Besides root biomass C input from actual root biomass, there is another source of OC input from the roots – rhizodeposition. Rhizodeposition is estimated to be half the root biomass of crops (Pausch and Kuzyakov 2018), and it depends on the degree of mycorrhizal colonisation since mycorrhiza can substitute functions of exudates (Jones et al. 2004). Neither rhizodeposition nor mycorrhization was included in this review as the data availability on this topic is extremely limited and would not allow for proper evaluation. Van de Broek et al. (2020) found no significant differences in net rhizodeposition between two old and two new wheat cultivars. A recent study by Chaplot et al. (2023) indicates that rhizodeposition differ by genotype. But there is no evidence that higher root biomass comes at the expense of rhizodeposition (Hirte et al. 2018; Pausch and Kuzyakov 2018). The key take away from this is that more studies on this topic are needed as we do not have enough reliable data on how rhizodeposition changes between different varieties. However, what we do know is that mycorrhizal colonisation varies between

genotypes. Al-Karaki and Al-Raddad (1997) found a higher mycorrhizal colonisation on a drought-resistant wheat genotype than on a drought-sensitive genotype. Singh et al. (2012) showed that the mycorrhizal colonisation varied depending on genotype and fertilisation intensity, demonstrating that rhizodeposition and its dependency on mycorrhizal colonisation is another factor that needs to be considered when estimating OC inputs from roots, but was neglected in this study. In general, root data are scarce and more research is needed if reliable conclusions are to be drawn.

Does genotype selection for increased root biomass compromise yield?

The data suggested that increased root biomass does not necessarily compromise yield (Fig. 3). In fact, the opposite was the case because there seemed to be broad potential for increasing root biomass without compromising yield in all crops. If farmers select the best yielding genotype, it is highly probable that they are also selecting for the highest root biomass C input. Mathew et al. (2019) showed that both aims of genotype selection – higher grain yields to sustain food production and higher root biomass C inputs for potentially increased C sequestration – can be achieved simultaneously. Notably, an increase of belowground biomass does not necessarily result in an equivalent decline of aboveground biomass as both are more likely to feed each other than not (Kell 2012). Poorter et al. (2012) suggested that biomass allocation might be controlled by the source and sink strength of all organs.

Grain yield was moderately positively correlated with root biomass under non-stressed conditions, but even more strongly and highly significantly positively correlated with root biomass and root:shoot ratio under drought stress (Mathew et al. 2019). In a similar experiment with 34 wheat genotypes, Severini et al. (2020) found that their own experiment had a much larger effect on the variation of biomass and yield than the genotype group. This led to the question of whether abiotic factors alter the yield and root biomass of genotypes even more than genetic variability. This knowledge gap could be filled by variety testing for climate change adaptation. Testing several genotypes under different climatic conditions without neglecting the "hidden part" of the plant could provide detailed insight into the actual possibilities and limitations of optimised genotype selection. Data on the roots of different genotypes at the maturity stage and corresponding yields are currently limited. More information on mature plants is needed because Bai et al. (2019) reported that laboratory seedling root screens did not predict the root growth of wheat genotypes in the field.

Roots are thought to play a key role when adapting food production to climate change (Kell 2012; Lynch and Wojciechowski 2015). Deeper rooting enhances water and nitrogen acquisition in many agroecosystems (Lynch 2013), while larger fine root proliferation and a higher mycorrhizal abundance in the topsoil increase phosphorus capture (Niu et al. 2013). But an increased root biomass does not necessarily equal a larger root system with benefits for resource acquisition and thus may not always be beneficial for the plant if under abiotic stress. Deeper crop rooting is also promoted as a C sequestration measure in the subsoil (Kell 2012; Lynch and Wojciechowski 2015). Optimised genotype selection and breeding towards generally more and/or deeper roots may thus enhance yield stability under future climatic conditions with increased drought events during their vegetation period in Europe.

Variation of root:shoot ratios – impact and potential of genotypes

The aboveground to belowground biomass, as displayed in the root:shoot ratio, is known to vary widely with environmental conditions and with management (Bolinder et al. 1997; Plaza-Bonilla et al. 2014; Keel et al. 2017). For example, the root:shoot ratio of conventional and organic winter wheat differed significantly from 0.09 (conventional) to 0.15 (organic) at flowering at eight field sites in Switzerland (Hirte et al. 2021). Even under homogeneous, optimal growth conditions in a greenhouse, the mean root:shoot ratio of 297 genotypes of spring wheat varied from 0.18 to 4.1 (Narayanan et al. 2014). The root:shoot ratios calculated in the present study are comparable to those mentioned above. The lowest root:shoot ratios ranged from 0.11 to 0.22 in Clermont-Ferrand, France and were higher in Hisar, India, where they ranged from 0.67 to 0.80. The included study by Mathew et al. (2019) reported significant variations among 100 genotypes of winter wheat, ranging from 0.03 to 3.04. Fang et al. (2017) also observed significant differences between three genotypes of winter wheat, which ranged from 0.61 to 1.13. In contrast, some studies found no

significant difference between root:shoot ratios of different genotypes (Bolinder et al. 1997; Xu et al. 2020; van de Broek et al. 2020). Van de Broek et al. (2020) conducted a mesocosm experiment that could have altered the root:shoot ratio in comparison with field experiments. The similar root:shoot ratios found by Bolinder et al. (1997) could be due to the genetic and functional equality of the genotypes.

Root:shoot ratios for silage maize ranged between 0.05 (Belgium, Ravels) and 0.19 (China, Lishu). These root:shoot ratios display the state at the time of maturity or harvest. Few comparable maize trials were found, but root:shoot ratios have been determined at earlier developmental stages. The root:shoot ratios of maize at the R1 growth stage ranged from 0.27 for unstressed maize plants to 0.47 for maize plants with 65 days of water stress in Akron, USA (Benjamin et al. 2014). Moreover, root:shoot ratios of eight maize genotypes varied from 0.4 to 0.7 at silking in Lusignan, France under field conditions (Hébert et al. 2001). In summary, root:shoot ratios might be generally lower in the present data owing to the plants being at a later developmental stage.

It was not possible to determine significant differences between the root:shoot ratios of genotypes. However, some crops appeared to be more flexible than others with regard to root:shoot ratios (Fig. 4, Table 5). Winter wheat in particular showed a broad range of root:shoot ratios not only between study sites, but also within them. In contrast, silage maize genotypes seemed very constant in root:shoot ratios. This suggests that some crops might be more favourable than others when aiming for more root biomass while maintaining yield levels. In crops with rigid root:shoot ratios such as maize, breeding might not be as successful as it might be when aiming for root biomass in flexible crops such as winter wheat. The validity is apparently limited by the scarce data situation, but a range of possible variabilities was still provided and attention drawn to the knowledge gap that limits theoretical estimations and the practical implementation of optimised genotype selection.

Implications

The selection of genotypes with a high root biomass production seems to be a promising easy-to-implement option for enhancing C inputs to agricultural soils, and may contribute to increase SOC stocks. The pressure on agriculture to decrease the CO_2 footprints of their products is increasing. Thus, C sequestration in soils is a much debated climate change mitigation measure that could help compensate for greenhouse gas emissions. However, many measures that increase soil C sequestration compromise yield and productivity. This review demonstrated that genotype selection is a feasible option for increasing root biomass C input to the soil while it could maintain or even enhance yields. Further, we identified a serious lack of data availability on differences in rhizodeposition between varieties of agricultural annual crops. Therefore, it was impossible to include rhizodeposition in this study constituting a considerable uncertainty when estimating root biomass C input to soils that must be addressed in future studies. Nevertheless, this review clearly demonstrated that there is a wide variation in root biomass and root:shoot ratio among genotypes, and breeders should start introducing root biomass as a new criterion for breeding. Additionally, increased root biomass due to deeper roots may stabilise yields under climate change conditions with increased frequency of drought events during vegetation periods, and may therefore serve as a climate change adaptation measure.

Declarations

Competing interests The authors have no relevant financial or non-financial interests to disclose.

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