

# Crops for increasing soil organic carbon stocks - A global meta analysis

Isack Mathew, Hussein Shimelis, Macdex Mutema, Budiman Minasny, Vincent Chaplot

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1 Crops for increasing soil organic carbon stocks - a Global Meta Analysis 2 Isack Mathew<sup>1</sup>, Hussein Shimelis<sup>1</sup>, Macdex Mutema<sup>2</sup>, Budiman Minasny<sup>3</sup>, Vincent Chaplot<sup>1</sup>, 3 4, \* 4 5 <sup>1</sup>University of KwaZulu-Natal, School of Agricultural, Earth and Environmental Sciences, 6 7 Private Bag X01, Scottsville 3209, Pietermaritzburg, South Africa, isackmathew@gmail.com; 8 <sup>2</sup>Agricultural Research Council-Institute of Agricultural Engineering, Private Bag X529, Silverton, Pretoria, South Africa, macdexo@gmail.com; 9 <sup>3</sup>Sydney Institute of Agriculture, School of Life and Environmental Sciences, The University 10 11 of Sydney, NSW 2006, Australia, budiman.minasny@sydney.edu.au 12 <sup>4</sup>Laboratoire d'Océanographie et du Climat: Expérimentations et approches numériques (LOCEAN). UMR 7159, IRD/C NRS/UPMC/MNHN, IPSL, 4, place Jussieu, 75252 Paris, 13 France, vincent.chaplot@ird.fr 14 15 \*Corresponding author: vincent.chaplot@ird.fr; Laboratoire d'Océanographie et du Climat: 16 **Expérimentations** numériques (LOCEAN). **UMR** 7159, IRD/C 17 et approches NRS/UPMC/MNHN, IPSL, 4, place Jussieu, 75252 Paris, France 18 19

#### Abstract

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Quantifying the ability of plants to store atmospheric inorganic carbon (C) in their biomass and ultimately in the soil as organic C for long duration is crucial for climate change mitigation and soil fertility improvement. While many independent studies have been performed on the transfer of atmospheric C to soils for single crop types, the objective of this study was to compare the ability of crops which are the most commonly found worldwide to transfer C to soils, and the associated factors of control. We performed a meta-analysis of 227 research trials, which had reported C fluxes from plant to soil for different crops. On average, crops assimilated 4.5 Mg C ha<sup>-1</sup> yr<sup>-1</sup> from the atmosphere with values between 1.7 Mg C ha<sup>-1</sup> yr-1, for barley (Hordeum vulgare) and 5.2 Mg C ha-1 yr-1 for maize (Zea mays). 61% of the assimilated C was allocated to shoots, 20% to roots, 7% to soils while 12% was respired back into the atmosphere as autotrophic respiration by plants. Maize and ryegrass (*Lolium perenne*) had the greatest allocation to the soil (1.0 Mg C ha<sup>-1</sup> yr<sup>-1</sup> or 19% total assimilation), followed by wheat (Triticum aestivum). 0.8 Mg C ha<sup>-1</sup> yr<sup>-1</sup>, 23%) and rice (Oryza Sativa, 0.7 Mg C ha<sup>-1</sup> yr<sup>-1</sup>, 20%). C allocation to the soil positively correlated to C allocation to roots C (r=0.33, P<0.05) while correlations between on the one hand shoot and root biomass and on the other hand C allocation to shoots were not significant. The question of the long -term stability of the C transferred to soils remains unanswered.

**Keywords**: Carbon transfer, C assimilation, plant C, C labeling, C flux

#### Introduction

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In 2015, 192 countries ratified the Paris Agreement at COP21 in Paris to limit the rise of 41 global air temperature to 2°C above pre-industrial levels by the end of this century (Minasny 42 et al. 2017). At that occasion, the 4 per mille Initiative: Soils for food security and climate 43 (4p1000) was launched by the French government with the aspiration to transfer atmospheric 44 carbon (C) to soils for a net increase in soil organic carbon (SOC) stocks (also termed soil 45 carbon sequestration, e.g. Chenu et 2019) by 0.4% per year (Minasny et al. 2017). The 46 Initiative envisaged that atmospheric C sequestration into soils would yield spillover benefits 47 such as reduced increase of global temperature, improved soil fertility; favorable soil 48 structure, high soil biodiversity, and reduced risk of soil erosion will accrue (Lal 2016) to 49 sustain higher crop productivity. 50 However, some practices proposed by Paustian et al. (2016) to meet the 4p1000 objectives, 51 52 such as reduced tillage and land use conversion, are subjects of debate. For example, it has been argued that reduced tillage only cause redistribution of SOC within the soil profile with 53 54 no net gain (Dimassi et al. 2014; Haddaway et al. 2017), while land use conversion from cropland to grassland or forest can have negative implications for SOC stocks and food 55 security. Furthermore, there is a high tendency to rely on best agronomic practices for 56 increasing SOC stocks, while neglecting the effects of plants despite abundant evidence that 57 genetic variation, especially in root traits, influences C allocation in terrestrial ecosystems 58 (Warembourg et al. 2003). 59 Carbon sequestration into soils is influenced by equilibrium C carrying capacity of the soil, 60 the vegetation it supports and the attendant climatic factors (Gupta and Rao, 1994; Lal, 2004). 61 Plants play a pivotal role in the global cycle because more than 10% of the carbon dioxide 62 (CO<sub>2</sub>) in the atmosphere is recycled through photosynthesis (Raich and Potter, 1995). After 63 photosynthesis, plants deposit organic C into the soil via exudation and biomass C 64

incorporation into the soil and a net increase in the soil C stocks is realized when the amount of C deposits are higher than C losses through microbial decomposition and root respiration (Fearnside and Barbosa, 1998). Plant C is either incorporated as structural C, released as exudates or respired as CO<sub>2</sub> (Ostle et al. 2003). These processes vary with crops' genetic characteristics, leading to potential differences in C fluxes to soils (Kuzyakov and Domanski 2000). Yet there is little empirical analysis on how crops differ in their ability to enhance SOC stocks (Wegener et al. 2015). The first step for assessing the ability of crops to sequester C in terrestrial ecosystems lies in the evaluation of the C fluxes to the different pools: shoots, roots and soil. There have been concerted efforts to understand C fluxes in the plant/soil system (e.g. Remus and Augustin 2016; Studer et al. 2014). Carbon fluxes are commonly estimated by measuring changes in SOC stocks over time (e.g. Hemminga et al. 1996). However, this method lacks precision when little changes in SOC stocks occur and is unable to distinguish between the preexistent and "new" SOC (e.g. Remus and Augustin 2016). Isotopic C labeling, where C 12 atoms are replaced with either C 13 or 14 atoms, facilitate the quantification of C fluxes from atmosphere to soil through plants (Studer et al. 2014). Based on C labelling, it has been reported that plants transfer from 30 to 50% of their photosynthetic C below ground (Buyanovsky and Wagner 1997). Furthermore, C labelling has proven that the translocation of C to roots may occur immediately after C assimilation in leaves with up to 10% of the photosynthetic C being detected in roots within 2 hours (Kaštovská and Šantrůčková 2007). Carbon assimilated by plants is allocated to above ground (shoots and reproductive organs) and below ground (roots) biomass depending onplant genetic constitution (de Neergaard and Gorissen 2004), plant growth pattern, environmental conditions and interactions among these factors (Rangel-Castro et al. 2005). However, it is the root C fluxes, which are particularly important for increasing SOC stocks because root tissues and/or root exudates are in

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immediate contact with the decomposer community and the mineral phase, thus leading to lower mineralization rates as compared to shoot-derived C (Rasse et al. 2005). Labile C inputs such as those derived from above ground biomass are potentially easily decomposed, leading to losses of the total plant C stock of 15-45% in case of perennial plants and 27-60% in annuals (e.g. Warembourg and Paul 1977; Swinnen et al. 1995a). Several compilations of individual studies have been performed to identify the trends in SOC dynamics (e.g., Guo and Gifford, 2002; Poeplau et al. 2011; Don et al. 2011). From Guo and Gifford (2002), we learn that the conversion of natural vegetation to cropland is detrimental to SOC stocks with a worldwide average loss in the 0-0.3m soil layer of 42% from native forest and of 59% from grassland. From this meta-study we also learn that afforestation of cropland can increase SOC stocks by as much as 50%, with Laganière et al., (2010) indicating greatest increase by using broadleaf tree species as compared to coniferous species. Meta-studies on land management impact on SOC stocks have also been performed. Poeplau and Don (2015) using 139 plots worldwide showed the potential of cover crops to increase SOC stocks in the first 0.2 m of the soil to be of  $0.32 \pm 0.08$  Mg C ha<sup>-1</sup> yr-<sup>1</sup> or about 0.5% or 5p1000. The study by Ugarte et al (2014) using data from 55 peer-reviewed studies showed a 9% average increase of SOC stocks in the 0-0.3 m layer using diversified crop rotations and conservation systems as compared to the conventional controls, a result confirmed by Alison et (2017). The increase was 32% by using a combination of chemical and organic fertilization (Han et al., 2016) as compared to no fertilization and Shi et al (2018) pointed to a 18% increase in SOC stocks using agroforestery under subtropical climate, all these studies considered the soil to a depth of 0.3m. While several individual studies worldwide have been published on the fluxes of atmospheric C to soils on one or several crops, these data have not been compiled yet and the global trends are still unknown.

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This study aimed at compiling multiple trials across the world that quantified C fluxes from the atmosphere to the soil during the growing cycle using C labelling. The hypothesis behind this study is that some crops might be more efficient than others to build SOC and might thus be promoted.

#### **Materials and Methods**

#### Meta analysis

The study is a meta-analysis based on data collated from isotopic C enrichment experiments conducted across the world. The data was obtained from peer-reviewed journal articles published between 1985 and 2016. The journal articles were obtained from academic databases (Google Scholar, Refseek, Science Direct, SciFinder, Scopus, Springer Link and Web of Science) using key words and phrases, singly and/or in combination, such as "isotopic pulse labelling", "C allocation", "plant carbon sequestration", "rhizodeposition" and "plants/soil/microbial respiration". The literature survey considered studies reporting the allocation of C to plant shoots and roots, soil pools and proportions of the respired C as either percentages or absolute quantities. Thirty-three journal articles (Table 1) detailing different studies were obtained using the above criteria providing 227 observations from different experiments, globally (Fig. 1). A database was constructed to capture the names of authors, year of publication, type of C isotope, type of crop, quantitative information on C allocation variables and the controlling factors (Supplemental Table).

#### The study variables, calculations and statistical analysis

This study simplified the soil-plant system within three pools, namely, plant shoots, plant roots, and soil. Information on C allocation to shoots (Sc), to roots (Rc), soil allocated C (Soc) and respiration from the soil (REc) (defined in Table 2) were collated from the different

studies. All these variables were estimated using the pulse labelling method where ambient <sup>12</sup>CO<sub>2</sub> was partially replaced by <sup>13</sup>CO<sub>2</sub> or <sup>14</sup>CO<sub>2</sub> for short durations. After harvest, plant parts (shoots and roots) as well as soil samples (collected from the pots in the case of glasshouse experiments or from the undisturbed soil in the case of field trials) were oven-dried (70°C). ground to 2 mm and analyzed for total C, <sup>13</sup>C or <sup>14</sup>C using C analysers coupled with mass spectrometers. Since the experiments differed as to the duration of pulse labelling, as to the concentration of labelled CO<sub>2</sub> and as the concentration of total CO<sub>2</sub>, the data of C allocation were normalized and transformed into single unit for unbiased comparison. Normalization was done by dividing the reported C allocations by the respective CO<sub>2</sub> concentration used during enrichment, duration of exposure during enrichment or the duration of that particular experiment, thus assuming the existence of linear relationship between the intensity of C fluxes in the atmosphere-plant-soil system and these variables. Moreover, in order to compare the crops' potential to transfer C to soils over an entire year, the data in different units were reported on a yearly basis by summing the fluxes observed during the growing months (i.e. few months in case of maize vs 12 months for permanent grasses), and harmonized as Mg C ha<sup>-1</sup> yr<sup>-1</sup>. Finally, the variations between field and greenhouse results were tested using the independent two-sample t-test at 95% confidence level using Genstat 18th edition (Payne et al. 2017). The parameters measured under field conditions were tested for normality and treated as independent samples from the greenhouse data and the two samples were regarded as heteroscedastic samples during the procedure for t-test (Yang et al 1992). Finally, the sample size for each variable was determined and stratified by crop type and environmental variable, namely soil texture, soil organic carbon content (SOCc) and average air temperature (Table 3). Summary statistics for the variables were derived including minimum, maximum, median, standard deviation (SD), skewness, 25<sup>th</sup> quartile (Q1) and 75<sup>th</sup>

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quartile (Q3), kurtosis and coefficient of variation. Afterwards, the data were summarized using box plots to elucidate the variability and distribution after checking out the outliers. Boxplots are presented for six major staple crops due to scarcity of data in the other crops. Bivariate and multivariate analyses, using Spearman rank correlations and principal component analysis (PCA), respectively, were conducted to depict the general relationships between C variables and some controlling factors.

# Results

Variability in	C Allocation	n to plant parts
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175	Table 4 presents the statistics of biomass and C allocation to the different plant parts from the
176	field and greenhouse trials. As shown by the statistical t test (Table 4), there was no
177	significant differences between field and greenhouse trials for all study variables, except for
178	root biomass (Rb), which was about two times higher under field conditions than in
179	greenhouses (36 vs 16 MgCha <sup>-1</sup> ).
180	The average C allocation to shoots ranged from 0.20 Mg C ha <sup>-1</sup> yr <sup>-1</sup> recorded by Swinnen et
181	al. (1995a) for barley in the Netherlands to 5.60 Mg C ha <sup>-1</sup> yr <sup>-1</sup> for wheat in Spain (Aljazairi et
182	al. 2015); the mean shoot C flux for all plant species was $2.48\pm0.09$ Mg C ha <sup>-1</sup> yr <sup>-1</sup> . The mean
183	C allocation to roots was 1.0 $\pm$ 0.04 Mg C ha <sup>-1</sup> yr <sup>-1</sup> with a lowest of 0.1 Mg C ha <sup>-1</sup> yr <sup>-1</sup>
184	calculated for sub-tropical wheat in Australia (Fan et al. 2016) and a highest of 2.8 Mg C ha <sup>-1</sup>
185	yr <sup>-1</sup> calculated for ryegrass in a temperate region of the USA (Butler et al. 2004). The lowest
186	total C allocation was 0.2 Mg C ha $^{\text{-}1}$ yr $^{\text{-}1}$ by wheat, while the highest was 22.1 Mg C ha $^{\text{-}1}$ yr $^{\text{-}1}$
187	by Kobresia spp. grass in temperate China (Wu et al. 2010). Mean C loss from soil as CO <sub>2</sub>
188	(autotrophic plus heterotrophic respiration) was 0.63±0.30 Mg C ha <sup>-1</sup> yr <sup>-1</sup> . Greenhouse grown
189	soyabean had the highest C emissions of 1.8 Mg C ha <sup>-1</sup> yr <sup>-1</sup> (Harris et. al. 1985). An average
190	of 0.90±0.05 Mg C ha <sup>-1</sup> yr <sup>-1</sup> was allocated to soils with a maximum of 3.00 Mg C ha <sup>-1</sup> yr <sup>-1</sup>
191	found for temperate maize in the USA (Holland et al. 1995). Environmental factors also
192	showed wide variability. The soil clay content ranged from 6.1 to 36.0%, while the SOCc
193	ranged from 2.70 to 37.00 g C kg <sup>-1</sup> . Temperatures varied from 5°C in the Netherlands
194	(Swinnen et al. 1995a) to 34.7°C in Spain (Fernández et al. 2003).

# Crop type impact on C allocation to shoot and roots

Figure 2 shows the variations in C allocation in the different pools (shoot, root, and soil) of the plant-soil system as function of crop type. The highest mean C allocation to shoots was observed in maize (4.10±0.12 Mg C ha<sup>-1</sup> y<sup>-1</sup>), which was 44% higher than for ryegrass (2.85±0.21 Mg C ha<sup>-1</sup> yr<sup>-1</sup>), which ranked second, and 91% higher than in barley (2.15±0.24 Mg C ha<sup>-1</sup> yr<sup>-1</sup>) with the lowest C allocation. The C allocation to shoot in wheat (2.52±0.20 Mg C ha<sup>-1</sup> yr<sup>-1</sup>) and rice (2.30±0.15 Mg C ha<sup>-1</sup> yr<sup>-1</sup>) were not significantly different. Ryegrass had at least 17% higher C allocation to shoots as compared to all the other crops except maize. The highest mean C allocations to roots were found in ryegrass (1.50±0.18 Mg C ha<sup>-1</sup> yr<sup>-1</sup>), followed by rice (1.48±0.17 Mg C ha<sup>-1</sup> yr<sup>-1</sup>) and maize (1.40±0.21 Mg C ha<sup>-1</sup> yr<sup>-1</sup>), but with differences being not significant at P<0.05 (Fig. 2b). In contrast, barley exhibited significantly (p≤0.05) lower C allocation to roots as compared to all the other crop species, while wheat and soyabean had intermediary C allocation to roots.

# Crop type impact on C allocation to the soil

Figure 3 compares the C allocation to the soil by the selected crops to the C allocation in the different plant parts, as a means to assess crop efficiency in allocating atmospheric C into soils. Soyabean had the largest proportion of C allocated to the soil as compared to the whole plant (ratio of 0.32±0.07, fig. 3a), which means that the amount of C recovered in the soil during the growing season is about a third of that recovered in the plant. Barley was the second most efficient crop because it transferred 0.29±0.06 units of C per unit of C fixed by the plant. Wheat, maize and rice showed similar efficiencies in terms of C transfer to the soil relative to the total C allocated in the plant (ratios between 0.18 and 0.20).

soyabean having the highest efficiency followed by barley (Fig. 3b). In contrast, barley and wheat had the highest C allocation to soils as compared to roots (ratio of 1.22, fig. 3b). The

least C allocation to soils per unit C allocation to roots was recorded in rice with a ratio of 222 0.48. Maize and soybean showed non-significant difference with means of 0.96 and 0.98, 223 respectively. Figure 3d shows the C allocation to soils relative to C emission from the soil as 224 CO<sub>2</sub> for the different crops. The highest ratio was observed for ryegrass (1.88±0.17) followed 225 by wheat  $(1.48\pm0.11)$ , maize  $(1.30\pm0.13)$  and barley  $(1.00\pm0.23)$ . 226 Figure 4 compares C allocation in the plant to C respiration from the soil. Ryegrass lost the 227 least amount of C through respiration relative to total plant C allocation (ratio of 0.11±0.01, 228 fig. 4a). For soyabean and barley, C respiration constituted above 40% of plant C allocation 229 while for the rest of the crop species this proportion was less than 20%. Soyabean had also the 230 highest ratio of respired C to shoot C allocation (0.85±0.13) which was 24% higher than for 231 ryegrass and with wheat showing the least ratio (Fig. 4b). Respired soil C as a fraction of C 232 allocation in roots was the highest barley and soyabean with 1.49±0.26 and 1.38±0.17, 233 234 respectively (Fig. 4c).

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# Variations in plant C allocation with soil properties and climate

#### Soil texture

Figure 5 shows the variations in C allocation in response to soil clay content. For clayey soils, the mean C allocation to shoots was 2.36±0.23 Mg C ha<sup>-1</sup> yr<sup>-1</sup> (Fig. 5a), which was 13% lower than that of loam textured soils (2.70±0.25 Mg C ha<sup>-1</sup> yr<sup>-1</sup>) with the widest variability (values between 0.5 and 4.6 Mg C ha<sup>-1</sup> yr<sup>-1</sup>). There was a decrease in root C allocation from clayey and loamy (1.30±0.13; 1.36±0.16 Mg C ha<sup>-1</sup> yr<sup>-1</sup>) to sandy soils (0.91 Mg C ha<sup>-1</sup> yr<sup>-1</sup>) (Fig. 5b). In contrast, soil respiration significantly decreased by 60% from sandy (0.75±0.12 Mg C ha<sup>-1</sup> yr<sup>-1</sup>) to clayey (0.47±0.03 Mg C ha<sup>-1</sup> yr<sup>-1</sup>) and sandy soils (0.46±0.04 Mg C ha<sup>-1</sup> yr<sup>-1</sup>), with the differences between clayey and sandy soils being not significant at P<0.05 (Fig. 5c).

The amount of isotopic C detected in the soil significantly and positively correlated with soil clay content (r=0.46, p<0.05). Figure 5d shows a general increase for isotopic C from 0.43±0.09 Mg C ha<sup>-1</sup>yr<sup>-1</sup> in sandy soils to 1.04±0.07 Mg C ha<sup>-1</sup> yr<sup>-1</sup> under loamy and 1.08±0.06 Mg C ha<sup>-1</sup> yr<sup>-1</sup> under clayey soils. The C detected in clay soils was nearly 150% higher than soil C fluxes under sandy soils.

#### Soil carbon content

SOC content exhibited a significant (p>0.05) and positive correlation with root C allocation (r=0.44) and with soil respiration (r=0.20, Table 5). Root C allocation was 33% higher from 0.79±0.08 Mg C ha<sup>-1</sup> yr<sup>-1</sup> under low SOCc to 1.07±0.08 Mg C ha<sup>-1</sup> yr<sup>-1</sup> under medium SOCc soils (Fig. 6b). Root C was 1.01 Mg C ha<sup>-1</sup> yr<sup>-1</sup> at higher SOCc, which did not correspond to a significant difference at p>0.05. Soil C allocation was with 1.01±0.16 Mg C ha<sup>-1</sup> yr<sup>-1</sup> the highest under medium SOCc and the lowest under low SOCc (0.84±0.06 Mg C ha<sup>-1</sup> yr<sup>-1</sup>). Finally, soil respiration did not significantly differ for all study SOCc classes (Fig. 6d).

#### Climate

Figure 7a shows that shoot C allocation was about 8% lower (2.32±0.23 Mg C ha<sup>-1</sup> yr<sup>-1</sup>) under cool climate than under warm conditions (2.51±0.13 Mg C ha<sup>-1</sup> yr<sup>-1</sup>) and was the lowest (2.18±0.08 Mg C ha<sup>-1</sup> yr<sup>-1</sup>) under hot temperatures. The difference between cool and warm climates was not significant. The weak negative correlation between temperature and shoot C fluxes was also revealed by the bivariate correlations (Table 5). In contrast, root C allocation and temperature were positively correlated (Table 5). An increase of over 53% in root C allocation was observed from 0.75±0.14 Mg C ha<sup>-1</sup> yr<sup>-1</sup> under cool to 0.99±0.12 Mg C ha<sup>-1</sup> yr<sup>-1</sup> under warm temperatures, while there was a sharp increase of 200% from warm to hot temperatures (1.51±0.15 Mg C ha<sup>-1</sup> yr<sup>-1</sup>) (Fig. 7b). The association between temperature and

soil respiration was relatively strong and positive (r=0.34; p $\leq$ 0.05) (Table 5). Carbon emissions due to respiration under warm (0.63 $\pm$ 0.01 Mg C ha<sup>-1</sup> yr<sup>-1</sup>) and hot (0.62 $\pm$ 0.02 Mg C ha<sup>-1</sup> yr<sup>-1</sup>) temperatures were similar, while they were significantly lower under cool temperatures (0.54 $\pm$ 0.05 Mg C ha<sup>-1</sup> yr<sup>-1</sup>) (Fig. 7c). Soil C allocation exhibited a negative correlation with temperature (Table 5, Fig. 7d). However, the differences in soil C allocation between cool (0.90 $\pm$ 0.08 Mg C ha<sup>-1</sup> yr<sup>-1</sup>) and warm (0.86 $\pm$ 0.05 Mg C ha<sup>-1</sup> yr<sup>-1</sup>) temperature zones were not significant and ranged between 0.58 $\pm$ 0.06 (Fig. 7c).

# Multivariate analysis

Principal component analysis (PCA) was conducted using the selected variables and data from all crop species. The first two principal components (Fig. 8) accounted for 68% of the data variability. The first principal component (Axis 1), which accounted for 40% of data variability, correlated the most with SOCc with positive coordinates. Since soil respiration had positive coordinates on Axis 1, it can be inferred that soil respiration increased with increasing SOCc. There was also a trend for soil respiration to positively correlate with C allocation in plant and in shoots. Principal component 2 (Axis 2), accounting for 28% of the variability in data, correlated the most with the shoot and plant biomass with positive coordinates, and air temperature and soil clay content with negative coordinates. The trend was thus for shoot and plant biomass to decrease with increase in air temperature and soil clay content. Moreover, as C allocation to soils and to roots showed negative coordinates on Axis 2, the trend was also for more C to be allocated to roots and to soils under clayey and warm conditions than under sandy and loamy soils of cooler climates. Interestingly, C inputs to roots and to soils appeared to decline with increasing shoot biomass.

#### Discussion

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The impact of crop species on C assimilation from atmosphere to shoots and roots

The wide variations in atmospheric C allocation to shoots from 0.4 to 5.6 Mg C ha<sup>-1</sup> yr<sup>-1</sup> was expected and is likely to result from variable environmental conditions, plant growth pattern and internal metabolism which are under genetic control (Staddon et al. 2004; Warembourg et al 2003). Maize exhibited a significantly higher assimilation of atmospheric C into shoots than ryegrass, which confirmed previous reports by Pausch and Kuzyakov (2017) and Atkinson et al. (2014). The differences in shoot C fluxes among annual crops could be partly due to variations in efficiency in C capture and internal C metabolism. For instance, maize has a higher leaf area and C4 photosynthetic pathway which render it more efficient in atmospheric C capture than C3 crops (wheat or rice), while its high concentration of lignin and hemicellulose result in the retention of more C in the shoots (Adapa et al. 2009; Li et al. 2013). The flux of C to roots in maize, rice and ryegrass was above 1.0 Mg C ha<sup>-1</sup> yr<sup>-1</sup>across all crop types, a result that is in agreement with the investigations by Huang and Johnson (1995) and Mathew et al. (2017). Root C allocation are influenced by genetic variations and/or growth habits with for instance ryegrass because of perennial growth storing a larger proportion of the assimilated C in its roots as compared to annual crops (Purdy et al. 2015). The high amount of C assimilated in maize roots is related to its high photosynthetic capacity which avails large amount of assimilates for translocation to the roots (Amanullah and Stewart 2013; Pausch and Kuzyakov 2017) after meeting demand in the above ground biomass (Ludewig and Flügge 2013). In case of rice, the high amount of C allocated to roots results from the plant's response to maintain root development under hypoxic conditions (Huang and Johnson 1995).

# The link between plant C fluxes and C transfer to the soil

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The existence of a significant correlation between root C allocation and C allocation to the soil (r=0.38; p≤0.05, table 5) is supported by prior knowledge showing that root derived C constitutes a substantial proportion of SOC (Rasse et al. 2005). Root C contributes to SOC through various ways, e.g., provision of C exudates which are eventually stabilized in the soil, physical protection of soils against erosion, formation of associations with mycorhizae for C immobilization in the soil and providing exchange site for chemical interactions between plant and soil ions (Rasse et al. 2005). Intuitively, higher C allocation to roots increases the potential for C transfer to soils as more root exudates are released into the soil. Crop species differ in the amounts of C allocation to the roots and in their root characteristics, which appeared in the present study to subsequently result in differences in the amount of C transferred to the soil by the different crop species. Ryegrass and rice exhibited high higher C allocation to the roots and to the soil, while maize and wheat showed high C allocation to soil (>0.8 Mg C ha<sup>-1</sup> yr<sup>-1</sup>) despite low root C allocation. The latter could point to the existence of mechanisms of regulation of C transfer to soils. Such mechanisms are beyond the scope of this paper but understanding these is required to identify crops for SOC sequestration. It was also interesting to observe that soyabeans had low C allocation to the soil (0.64 Mg C ha<sup>-1</sup> yr<sup>-1</sup>) despite having high root C allocation. This points to the relative inefficiency of legumes to build SOC. Microbial respiration, which returns C to the atmosphere as shown by the high Rec (Fig. 2d), can be implicated in the low C sequestration potential of legumes. In the short term, soil C sequestration under annual crops such as maize may be higher than perennials such as ryegrass because C exudation below ground in annual crops peaks earlier during plant development than in perennials (Pausch and Kuzyakov 2017). Conversely, ryegrass is likely to contribute more biochemically stable C to soils through root turnover rather than exudation (Menichetti et al. 2015; Mota et al. 2010). Chemical, physical and matter with low C:N ratio, like soyabean shoots are easily decomposed by microbes to become SOC as compared to crop residues with high C:N such as from cereals (Abiven et al. 2009).

From Hütsch et al. (2002) we learn that only up to 5% of the C assimilated by plants is eventually stabilized in the soil after accounting for respiration. Based on estimations after harvest in the current study, C transfer to the soil reached 32% of net plant total C assimilation in soyabean, followed by barley (28%) and wheat (23%), while values for maize, ryegrass and rice reached 19% of their assimilated C to the soil. The question of the longer term stabilization of this newly assimilated SOC remains unanswered. There is also a need to conduct more investigations to assess the longer term impacts of rhizodeposition of energy-rich substrates in deep soil horizons on the mineralization of pre-existent "old" soil organic matter, by a process called rhizosphere priming effect (e.g. Fontaine et al., 2004; Shahzad et al, 2018).

biochemical processes influence the amount of C stabilized in the soil. For instance plant

# The link between C assimilation in the soil and soil CO<sub>2</sub> emissions

The study showed no significant correlation between C assimilation in the soil and soil CO<sub>2</sub> emissions suggesting that addition of C does not necessary enhance C losses through respiration in the short term, which may be explained by a possible mechanism that offers a relatively higher protection of the newly assimilated C. There were large differences in C emissions from soils with, for example, soyabeans emitting 1.12 Mg C ha<sup>-1</sup> yr<sup>-1</sup> while ryegrass grass emitted significantly lower amounts (0.49 Mg C ha<sup>-1</sup> yr<sup>-1</sup>). The high amount of C emission under soyabean may be explained as mentioned above by a low C:N ratio and associated high microbial respiration (Schmitt et al. 2013) as compared to cereals (Pausch and Kuzyakov 2017). The higher soil CO<sub>2</sub> emissions under maize (0.9 Mg C ha<sup>-1</sup> yr<sup>-1</sup>) are most

likely because of high hemicellulose-content biomass (Adapa et al. 2009; Li et al. 2013) and low C:N ratio as compared to barley and wheat (Velthof et al. 2002). Despite higher soil CO<sub>2</sub> emissions, maize exhibited a higher C allocation to soils than wheat, barley and rice showing that it is more efficient in photosynthesis (Amanullah and Stewart 2013) than the other crops. This shows that soil C accumulation can still be driven by root C allocation provided they are high enough to offset soil CO<sub>2</sub> emissions. The foregoing indicates that maize and ryegrass had superior ability for C allocation into the soil than the other plant species, while wheat appeared to be the most efficient among the winter crops such as barley.

#### The effect of environmental conditions on C allocation into soils

The results pointed to a lack of significant impact of the type of experiment performed (field vs glasshouse) on the study variables, except for root biomass which was about two times higher under field conditions (with mean of 36 MgCha<sup>-1</sup>) compared to the greenhouse (16 MgCha<sup>-1</sup>). Such a lack of significant differences is indicative of the absence of major shifts in the environmental conditions at glasshouses as compared to fields. Moreover, the greater root biomass under field conditions might be explained by the fact that under field conditions the roots have more room to growth as compared to greenhouse where the root zone is constrained by the pot size.

The positive association between soil C sequestration and clay content (r=0.46; p≤0.05) (Table 5) and the fact that clayey soils stabilized 200% more soil C than sandy soils (Fig. 5d) show the importance of soil clay fractions in C dynamics. Clay particles provide adsorption and aggregation sites for the intrinsic stability of C compounds and protection from microbial decomposition, which increases persistence of organic C in fine-textured soils in comparison with coarse texture soils (Hütsch et al. 2002).

The lack of a significant correlation between soil C sequestration and temperature was rather surprising and contrary to other study reports (e.g. Davidson and Janssens 2006; Jones et. al. 2005). However, temperature may have impacted soil C indirectly by increasing soil moisture, soil CO<sub>2</sub> emissions and by promoting high C retention in the root biomass as Giardina et al. (2014) reported that high temperatures promote root C accumulation to maintain vital biological processes.

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# Implications of cropping systems on soil C dynamics

Isotopic tracing techniques have shown that after fixation of atmospheric by plants, C allocation occurs to below ground biomass occurs within a few hours period (Gregory et al. 1991). The C dynamics in the soils are immediately affected by exudation, respiration and immobilization to variable extents depending on the soil and plant characteristics. Root respiration is essential for plant growth although it results in loss of fixed C and represents a return loop for CO2 back into the atmosphere. The results of this meta-analysis show that on average 7% of the atmospheric C fixed by plants will be stabilized into the soils while 12% was respired back into the atmosphere as autotrophic respiration by plants. The proportion varied with crop species. For instance, wheat allocated the highest proportion (23% total assimilation) of fixed C to the soil. This study reported that maize and ryegrass could potentially deposit 1.0 Mg C ha<sup>-1</sup> yr<sup>-1</sup> into the soil, followed by wheat (0.8 Mg C ha<sup>-1</sup> yr<sup>-1</sup>), and rice (0.7 Mg C ha<sup>-1</sup> yr<sup>-1</sup>), showing that impact that different cropping systems could have on soil C dynamics depending on other factors such as agronomic practices. Qiao et al (2012) and An et al (2015) provided evidence that plants increased SOC but alluded to the effects of fertilizer application and mulching, which increased C sequestration potential in soybeans and maize. The impact of crops on soil C dynamics is also governed by the species as Fan et al (2008) reported that maize distributed higher proportion of C below ground compared to faba beans although the distribution dynamics changed when the intercropping system was altered showing that C sequestration is also influenced by synergies or competition between and among crop communities. Fang et al (2016) investigated the impact of tillage practices on C sequestration and concluded that SOC stocks and agronomic functionality could not be improved by conservation tillage only. Plants were therefore the critical conduit for C sequestration into soil. Qiao et al (2012) found that soybean could potentially deposit 160 to 564 kg ha<sup>-1</sup> C season<sup>-1</sup> in China. In comparison, Mutegi et al (2011) estimated barley could contribute up to 3.4 Mg C ha<sup>-1</sup>, which was 600kg shortfall to maintain long term soil organic C in Denmark. In essence, there is overwhelming evidence to show the potential of crops in increasing C in the soil. The most important issues surrounding C allocation to soils are centered on the quantities of C sequestered, the mean residence time of the deposited C and the cost benefit of C sequestration by plants against the C emission during agricultural operations such as ploughing and fertilization.

# **Conclusions**

- Three main conclusions can be drawn from this study of 227 research trials worldwide investigating atmospheric C allocation to crop shoots, roots and to the soil:
- (i) (i) Only a small fraction (about 7%) of the plant assimilated C is found in the soil after harvest with wheat showing the highest proportion (23%), followed by rice (20%), and maize and ryegrass with 19%;
- (ii) (ii) The transfer of atmospheric C to the soil was the highest for maize (1.00 Mg C ha<sup>-1</sup> yr<sup>-1</sup>) followed by ryegrass (0.95 Mg C ha<sup>-1</sup> yr<sup>-1</sup>), rice (0.70 Mg C ha<sup>-1</sup> yr<sup>-1</sup>), and wheat (0.80 Mg C ha<sup>-1</sup> yr<sup>-1</sup>);
- 441 (iii) Irrespective of crop type, higher SOC was recorded under clayey soil and 442 warmer climates.

Such quantitative information on C allocation by plants and to soils might be used by C models for improving crop selection and/or rotations for enhanced atmospheric C sequestration, soil fertility and crop production, from short to long term. These results could also be used in selecting crop genotypes of higher soil C sequestration potential, which could be useful in informing the breeding efforts to enhance the genetic capacity of existing crops. More is however to be done on the long term stability of the C allocated to soils and on the mechanisms involved in the C transfer from roots to its stabilization into soils. There is also a need to identify the genetic markers associated with the key traits for C allocation in the different plant parts and into the soil to further marker-assisted breeding and trait introgression into agronomically desirable genotypes that would potentiate C storage without compromising grain yield and grain quality.

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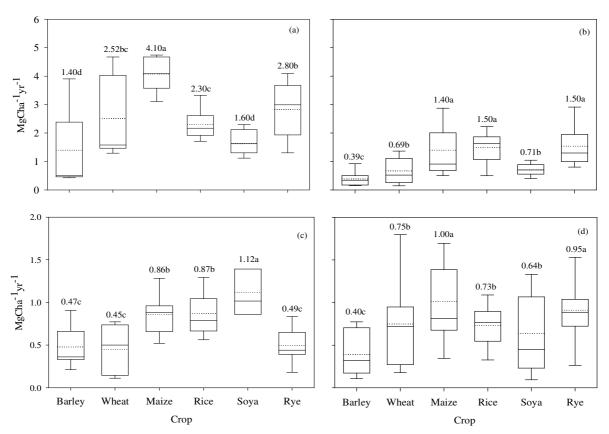
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681	in a Kobresia grassland on the Qinghai-Tibetan Plateau revealed by field 13C pulse-
682	labeling. Global Change Biology, 16(8): 2322-2333
683	Yang SR Koo, WW, Wilson, WW (1992) Heteroskedasticity in crop yield models. Journal of
684	Agricultural and Resource Economics, 103-109



Fig. 1 Global distribution of the study sites shown by shaded circles on the map



**Fig. 2** Carbon allocation into (a) Sc: shoots, (b) Rc: roots; c) REc: soil respiration and (d) SOc: C allocation to the soil; as affected by crop species. Rye=ryegrass and Soya=soyabean. Values above the top whisker represent mean values of each crop. Means followed by the same letters are not significantly different at  $p \le 0.05$ .

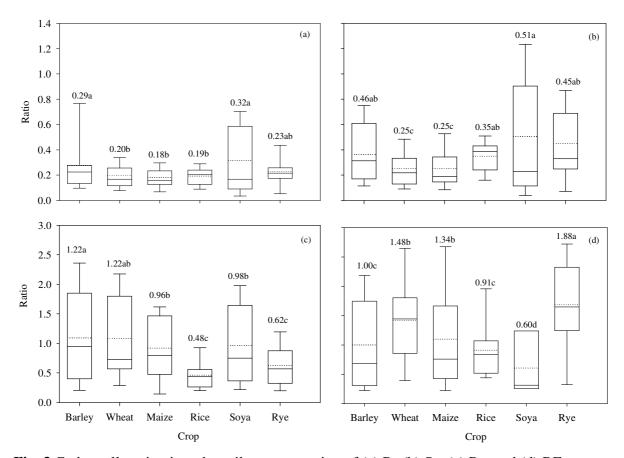


Fig. 3 Carbon allocation into the soil as a proportion of (a) Pc (b) Sc, (c) Rc, and (d) REc.

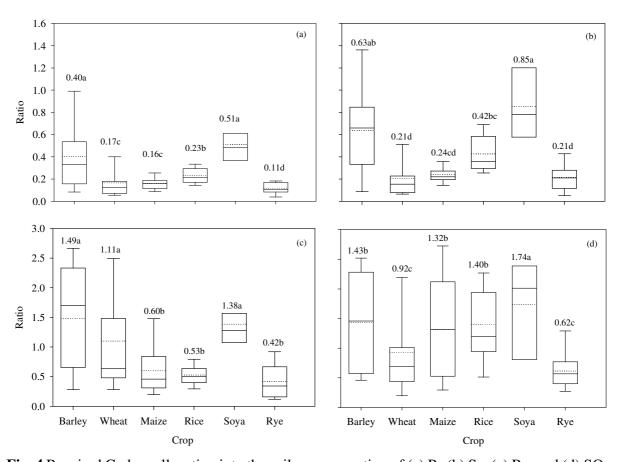


Fig. 4 Respired Carbon allocation into the soil as a proportion of (a) Pc (b) Sc, (c) Rc, and (d) SOc.

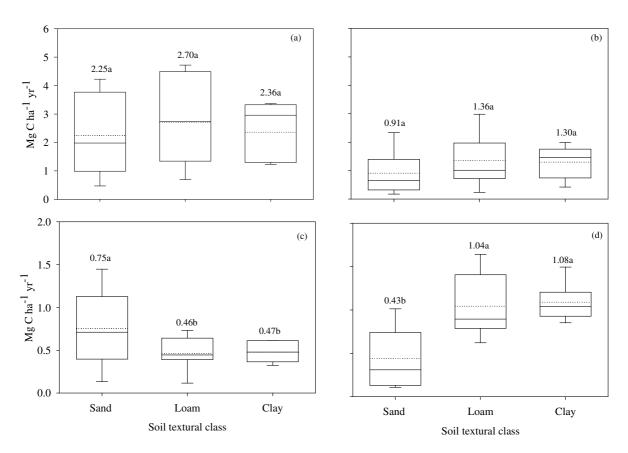
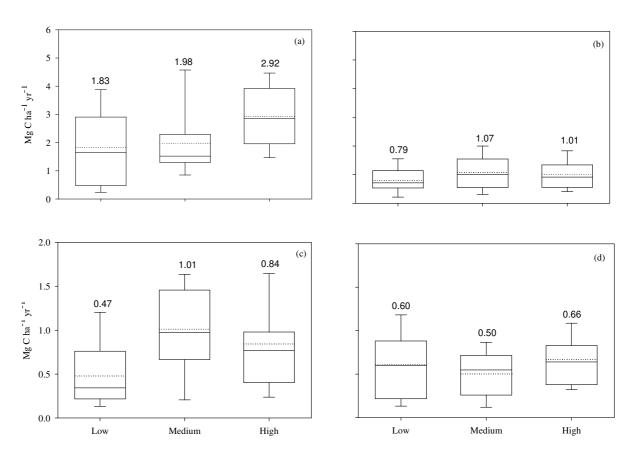
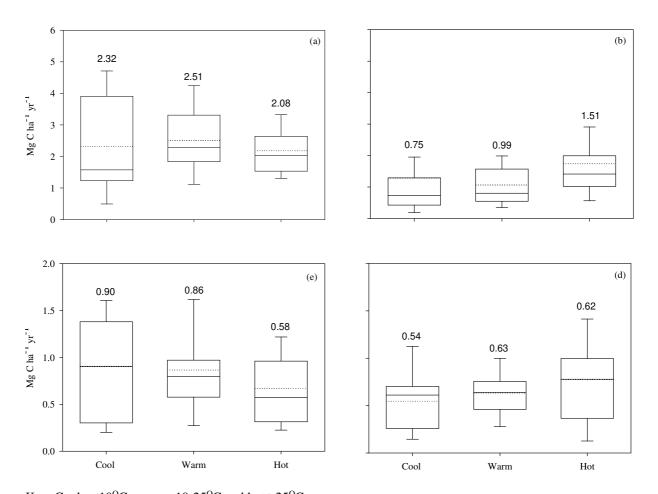


Fig. 5 Carbon allocation into (a) Sc (b) Rc, (c) REc, and (d) SOc.



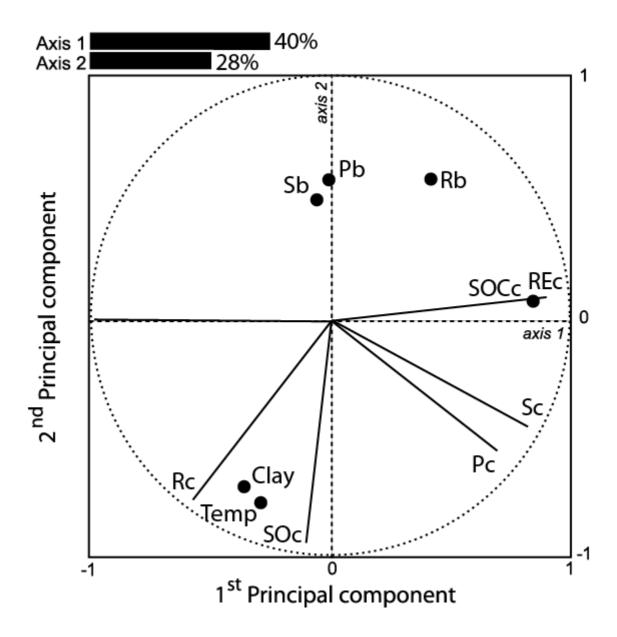
key: Low= $<10gCkg^{-1}$ , medium= $10-15gCkg^{-1}$  and high= $>15gCkg^{-1}$ 

 **Fig 6** Impact of soil organic carbon content (SOCc) on carbon allocation into (a) Sc, (b) Rc, (c) SOc, and (d) REc. See table 2 for SOCc classes.



Key: Cool=  $<10^{\rm O}$ C, warm= 10- $25^{\rm O}$ C and hot  $>25^{\rm O}$ C

**Fig 7** Impact of air temparature on carbon allocation into (a) Sc, (b) Rc, (c) SOc, and (d) REc. See table 2 for SOCc classes.



**Fig 8** PCA showing multivariate relationship among variables and factors all plant types. Sc=shoot C allocation, Rc=root C allocation, SOc=soil C allocation, REc=soil respiration, Rb=root biomass, Pb=plant biomass, Rb/Sb=biomass root:shoot, Temp=temperature and SOCc=soil organic C content. See Table 2 for full description of variables.

Table 1 List of authors, countries, crop types studied and type of experiment carried out using an identified carbon isotope

No.	Author	Country	Isotope	Crop	Experiment	Soil
						cm
1	Aljazairi et al. 2015	Spain	13C	Cereal	Greenhouse	
2	An et al. 2015	China	13C	Cereal	Field	0-15
3	Aranjuelo et al. 2009	Spain	12C	Cereal	Greenhouse	
4	Bazot et al. 2006	Switzerland	14C	Grass	Field	NA
5	Butler et al. 2004	USA	13C	Grass	Greenhouse	
6	Chaudhary et al. 2012	USA	13C	Grass	Greenhouse	
7	Davenport and Thomas 1988	Canada	14C	Cereal, grass	Greenhouse	
8	de Graaf et al. 2009	USA	13C	Cereal	Greenhouse	0-25
9	de Neergaard and Gorissen	Denmark	14C	Grass, legume	Greenhouse	
10	Domanski et al. 2001	Germany	14C	Grass	Greenhouse	
11	Fan et al. 2008	China	13C	Cereal, legume	Greenhouse	
12	Fang et al. 2016	Australia	13C	Cereal	Field	0-30
13	Fernández et al. 2003	Spain	14C	Cereal	Greenhouse	
14	Gocke et al. 2011	Germany	14C	Cereal, grass	Field	NA
15	Gregory and Tawell 1991	Australia	14C	Cereal	Field	0-15
16	Harris et al. 1985	USA	14C	Legume	Greenhouse	
17	Hodge and Millard 1998	UK	14C	Cereal	Greenhouse	
18	Hodge et al. 1997	UK	14C	Grass	Greenhouse	
19	Holland et al. 1995	USA	14C	Cereal	Greenhouse	
20	Kaiser et al. 2015	Australia	13C	Cereal	Greenhouse	
21	Kakiuchi and Kobata 2008	Japan	14C	Legume	Greenhouse	
22	Lodhi et al. 2009	Pakistan	14C	Cereal	Greenhouse	
23	Meng et al. 2013	China	13C	Cereal	Greenhouse	
24	Mutegi et al. 2011	Denmark	14C	Legume	Field	0-10;
25	Qiao et al. 2012	China	13C	Legume	Field	NA
26	Schmitt et al. 2013	Germany	14C	Grass	Greenhouse	
27	Schulze and Poschel 2004	Germany	14C	Cereal	Greenhouse	
28	Swinnen et al. 1995	Netherlands	14C	Cereal	Field	0-20
29	Tian et al. 2013	China	14C	Cereal, grass	Greenhouse	
30	Warembourg et al. 2003	France	14C	Legume, cereal	Greenhouse	
31	Werth and Kuzyakov 2006	Germany	14C	Cereal	Lab	
32	Wu et al. 2008	China	13C	Cereal	Greenhouse	
33	Wu et al. 2010	China	13C	Grass	Field	NA

Table 2 Definition of C allocation variables and controlling factors as used in this paper

Parameter	Units	Definition	Categories	Remarks	
Shoot carbon allocation (Sc)	MgCha <sup>-1</sup> yr <sup>-1</sup>	The amount of C allocated to the shoots	Shoot	All crops used in the study	
Root carbon allocation (Rc)	MgCha-1yr-1	The amount of C allocated to the roots	Root	All crops used in the study	
Plant C allocation (Pc)	MgCha-1yr-1	Sum of the shoot and root C allocations	Plant	All crops used in the study	
Soil carbon allocation (SOc)	MgCha <sup>-1</sup> yr <sup>-1</sup>	The amount of C allocated to the soil	Soil	All crops used in the study	
Respired carbon from soil (REc)	MgCha <sup>-1</sup> yr <sup>-1</sup>	The amount of C being respired from the soil	Soil respiration	All crops used in the study	
			Cereals	All monocot grain crops	
Crop type		The broad group to which a plant belongs	Legumes	All N fixing plants	
			Grasses	All pasture grasses	
Shoot biomass (Sb)	Mgha <sup>-1</sup> yr <sup>-1</sup>	The annual total amount of above ground biomass (leaves and stems) excluding grain lint or pods	All	All crops used in the study	
Root biomass (Rb)	Mgha <sup>-1</sup> yr <sup>-1</sup>	The annual total amount of biomass found below the soil surface (crown roots, rhizoms and nodules) excluding stems and leaves.	All	All crops used in the study	
Plant biomass (Pb)	Mgha <sup>-1</sup> yr <sup>-1</sup>	The sum of root and shoot biomass	All	All crops used in the study	
			Sand	below 20%	
Clay content (Cl%)	%	The clay fraction of the soil	Loam	between 20-30%	
			Clay	above 30%	
			Low	below 10 g C kg <sup>-1</sup>	
Soil Organic Carbon content (SOCc)	g C kg <sup>-1</sup>	The C content of the soil at the start of the experiment	Medium	between 10 and 15 g C kg <sup>-1</sup>	
,			High	above 15 g C kg <sup>-1</sup>	
			Cool	up to 10°C	
Temperature (Temp)	°C	The average temperature during CO <sub>2</sub> enrichment	Warm	between 10 and 20 °C	
			Hot	above 20 °C	

**Table 3** Sample size of C allocation variables stratified by different factors

\$7	D	Sc	Rc	REc	C <sub>seq</sub>	C <sub>seq</sub> /Sc	C <sub>seq</sub> /Rc		REc/Rc	C <sub>seq</sub> /Sb	
Variable Crop type	<b>Description</b> Cereal	<b>200</b> 130	<b>194</b> 124	142 95	153 96	153 96	153 96	95	136 89	138 96	138 96
Crop type	Grass	47	47	36	36	36	36	36	36	24	24
	Legume	22	22	10	20	20	20	10	10	18	18
	Non-legume	1	1	1	1	1	1	1	1		
Soil texture	Clay	19	19	7	11	11	11	7	7	4	4
	Loam	39	39	23	31	31	31	23	23	31	31
	Sand	14	14	14	14	14	14	14	14	14	14
	Unclassified	128	122	98	97	97	97	98	92	89	89
SOCc (g C kg <sup>-1</sup> )	High	35	35	21	27	27	27	21	21	27	27
	Low	16	16	6	10	10	10	6	6	10	10
	Medium	17	17	4	6	6	6	4	4	6	6
	Unclassified	132	126	111	110	110	110	111	105	95	95
Temperature (°C)	Cool	49	49	37	49	49	49	37	37	38	38
	Hot	36	36	10	20	20	20	10	10	20	20
	Warm	89	83	73	74	74	74	73	67	70	70
	Unclassified  Regreat C flys: St	26	26	22	10	10	10	22	22	10	10

Sc=shoot C fluxes; Rc=root C flux; SOc=soil C flux; REc=respiration C flux; SOc:Sc, SOc:Rc, REc:Rcs, SOc/Sb and SOc/Rb are ratios of the respective variables

Table 4. Summary statistics on plant parameters, C allocation to plant parts and soil parameters based on data collected from field and greenhouse evaluations.

		C allocation						Soil parameters										
	S	Sb	R	lb	F	Pb	Rb/Sb			Sc	Rc		Pc		Clay		SOCc	
	Mgha <sup>-1</sup>						Mgyr <sup>-1</sup> ha <sup>-1</sup>					%		gkg <sup>-1</sup>				
Statistics	FD	GH	FD	GH	FD	GH	GH	FD	FD	GH	FD	GH	FD	GH	FD	GH	FD	GH
Observations	34	87	34	84	34	87	34	114	81	114	71	129	81	114	36	17	22	45
Mean	124.7	152.2	36.6	16.6	161.30	168.30	0.505	2.545	2.32	2.55	0.97	1.07	4.30	4.63	21.94	20.78	10.89	17.28
Variance	69923	349708	2388	1292	81764	351412	0.17	1.57	1.71	1.57	0.33	0.66	19.95	7.10	80.21	108.66	7.56	59.93
St dev	264.40	591.40	48.86	35.94	285.90	592.80	0.4196	1.2531	1.31	1.25	0.58	0.81	4.47	2.67	8.96	10.42	2.75	7.74
SEM	45.35	63.40	8.38	3.92	49.04	63.55	0.072	0.117	0.15	0.12	0.07	0.07	0.50	0.25	1.49	2.53	0.59	1.15
t value	-0.	.35	2.16		-0.09		-14.82		-1.21		-1.01		-0.59		0.42		-4.93	
df	1	116 48		114 144		193 18		35	5 120		51		61					
p-vlaue	0.725ns 0.036*		0.9	3ns	0.001**		0.228ns		0.313ns		0.559ns		0.678ns		0.001**			

<sup>\*</sup> and \*\* denote significant difference at P<0.05 and p<0.01, respectively; ns=non-significant difference. df=approximate degrees of freedom, FD=field condition, GH=greenhouse condition, SEM=standard error of mean, St dev=standard deviation. Sb=shoot biomass, Rb=root biomass, Pb=total plant biomass, Rb/Sb=root to shoot ratio, Sc=C allocation to shoot, Rc= C allocation to root, Pc= C allocation to plant, SOCc=soil organic carbon content.

In the materials and methods were need to mention that the variation between field and greenhouse data was tested using the independent two-sample t-tests at 95% confidence level using Genstat 18<sup>th</sup> edition. The parameters measured under field conditions were treated as independent samples from the greenhouse data and the two samples were regarded as heteroscedastic samples during the procedure for t-tests (Yang et al 1992).

Yang, S. R., Koo, W. W., & Wilson, W. W. (1992). Heteroskedasticity in crop yield models. Journal of Agricultural and Resource Economics, 103-109.

**Table 5** Spearman rank correlation coefficients showing pair-wise relationship among C flux variables and controlling factors used in the study for all crops

	Temp	Cl%	SOCc	Sb	Rb	Sc	Rc	Cseq	REc	C <sub>seq</sub> :Sc	C <sub>seq</sub> :Rc	REc/Sc	REc:Rc	C <sub>seq</sub> /Sb	C <sub>seq</sub> /Rb
Variables															
Temp	1.00														
Cl%	0.66*	1.00													
SOCc	0.23*	0.91*	1.00												
Sb	-0.15	-0.79*	-0.66*	1.00											
Rb	-0.03	-0.61*	-0.37*	0.80*	1.00										
Sc	-0.04	-0.11	0.20	0.02	-0.20*	1.00									
Rc	0.04	0.21*	0.44*	-0.12	0.04	-0.01	1.000								
$\mathbf{C}_{seq}$	-0.01	0.46*	0.11	-0.13	-0.18	0.11	0.38*	1.00							
REc	0.34*	-0.28*	0.20*	0.09	0.09	0.19*	0.33*	-0.12	1.00						
$C_{seq}$ :Sc	0.04	0.40*	0.48*	-0.17	-0.05	-0.51*	0.33*	0.75*	0.01	1.00					
C <sub>seq</sub> :Rc	-0.14	0.07	-0.23	-0.04	-0.14	0.22*	-0.67*	0.35*	-0.23*	0.18*	1.00				
REc/Sc	0.11	-0.26	0.49*	0.05	0.12	-0.59*	0.23*	-0.02	0.57*	0.41*	-0.31*	1.00			
REc:Rc	0.02	-0.19	-0.16	0.11	0.24*	0.03	-0.78*	-0.34*	0.25*	-0.31*	0.62*	0.18*	1.00		
C <sub>seq</sub> /Sb	0.01	0.04	0.01	0.10	0.12	0.02	0.03	0.72*	0.13	0.69*	0.58*	0.13	0.05	1.00	
C <sub>seq</sub> /Rb	0.04	-0.35*	-0.10	0.24*	0.22*	0.11	-0.08	0.59*	0.19	0.48*	0.58*	-0.03	0.16	0.88*	1.00

<sup>\*=</sup>significance at p≤0.05

Temp=temperature; Cl%=soil clay content; SOCc=soil organic carbon content; Sb=shoot biomass; Rb=root biomass; Sc=shoot C fluxes; Rc=root C fluxes; Soc=soil C fluxes; REc=respiration C fluxes; SOc:Sc, SOc:Rc, REc/Scs, REc:Rcs, SOc/Sb and SOc/Rb are ratios of the respective variables