

Quantifying direct yield benefits of soil carbon increases from cover cropping

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Cropland management practices that restore soil organic carbon (SOC) are increasingly presented as climate solutions that also enhance yields. But how often these benefits align at the farm level—the scale of farmers’ decision making—remains uncertain. We examined concurrent SOC and yield responses to cover cropping, including their direct connection, with a global meta-analysis. Cover cropping simultaneously increased yields and SOC in 59.7% of 434 paired observations. Increases in SOC directly increased crop yields in soils with initial SOC concentrations below 11.6 g kg⁻¹; for example, a change from 5 g kg⁻¹ to 6 g kg⁻¹ increased yields by +2.4%. These yield benefits of SOC did not decline as nitrogen inputs increased or when legume cover crops were used, suggesting fertility inputs cannot substitute for SOC effects. Regardless of direct effects of SOC increases on yields, integrating legume cover crops into systems with simplified rotations or with nitrogen inputs < 157 kg ha⁻¹ season⁻¹ N led to the largest yield increases (up to +24.3%), with legumes also increasing SOC more than non-legumes (up to +1.5 g kg⁻¹). By simultaneously increasing yields and SOC, cover cropping provides an opportunity to benefit both food security and climate, including via direct yield benefits from SOC increases on low carbon soils.

Soil organic carbon (SOC) is considered a critical component of soil health. In agroecosystems, soil health is a metaphor that describes the degree to which soils support multiple functions beyond crop productivity^{1,2}. SOC influences multiple soil-based ecosystem services, such as nutrient cycling and retention, soil aeration and structure³, climate regulation⁴ and possibly crop productivity⁵. The concentration of SOC has thus become one of the most common metrics for assessing soil health⁶.

Despite the various benefits that SOC is thought to provide⁷, agricultural expansion and intensification have dramatically depleted SOC across the world⁸. Practices that sequester SOC, defined here as when soil carbon inputs are greater than outputs, are garnering increasing attention for their potential to restore soil functionality while simultaneously drawing down atmospheric carbon dioxide^{9,10}. Cover cropping is one such practice. Grown on fallow soils otherwise left bare,

cover crops increase organic matter inputs to the soil in the form of crop detritus and root exudates. Recent meta-analyses showed that cover cropping increases SOC by 0.21–0.56 MgC ha⁻¹ yr⁻¹ (refs. 11–13), highlighting its potential to restore some portion of the 116 Pg of global SOC that has been lost since the dawn of agriculture⁸.

Yet the extent to which farmers will voluntarily adopt carbon sequestering practices hinges on more than just their potential to mitigate climate change or restore soil health^{14,15}. How a practice influences crop productivity and farm profitability is central to farmers’ management decisions. Recent meta-analyses and remote-sensing studies show that cover cropping variably affects crop yields^{16,17}, with estimates ranging from increases of 6% to 33%, depending on cash crop type, cover crop type, fertilizer additions and other factors such as aridity¹⁸, to small yield decreases^{19,20}. Since syntheses of how cover cropping affects SOC and yields have been conducted separately, it is

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not known how often cover cropping simultaneously increases SOC and yields at the same location (co-benefits), increases or decreases one but not the other (trade-offs), or even decreases both SOC and yields (co-costs). Understanding the potential for co-benefits will help inform decision making at the farm level and identify areas of overlap between benefits for farms and benefits for society.

Perhaps more important, it is not known whether there are management, edaphic or environmental conditions in which the largest yield increases are most likely to align with the largest SOC increases. Likewise, when yield increases do result from cover cropping, a critical knowledge gap is the relative role of changes in SOC in driving these increases, versus other cover cropping effects, such as nutrient scavenging²¹. Understanding the role that SOC plays in yield changes under cover cropping would contribute to recent calls to better quantify the relationship between SOC and yields generally^{5,22}.

The widespread expectation that increasing SOC will increase crop productivity exists^{8,23–25} because, as part of soil organic matter, SOC is related to many soil properties and functions that are important for plant productivity such as nutrient and water provisioning. However, evidence of a relationship between SOC and yield remains contradictory and inconclusive^{5,26–28}. Pot experiments show a positive and causal relationship between SOC and plant growth, with a threshold of -30 g kg^{-1} SOC^{29,30}, but limited external validity—beyond the direction of causality—is reasonable from few controlled environment studies that artificially manipulate SOC. Other attempts to circumvent this challenge use observational data, but the lack of controls and covariation between SOC and other environmental and management variables create complex interactions that can be difficult to tease apart, even using multivariate approaches^{5,26}. Using similar observational data-based meta-analytic techniques, recent studies have reported positive effects of SOC on yield^{5,28}, little to no effects²⁶ and negative effects²⁷. In addition, observational studies examining SOC-to-yield relationships span very wide ranges of SOC^{5,28}. These regional or global SOC-to-yield relationships are generally not applicable to an individual farmer since SOC increases following changes to management are often modest (for example, relative increases of 5–6% SOC for cover cropping and reduced tillage³¹).

Meta-analysis of studies on agricultural practices expected to shift SOC, such as cover cropping, provides an alternative approach to quantifying the SOC-to-yield relationship⁵. By pairing treatments with relevant control values, relationships between changes in SOC and changes in yield can be quantified in such a way that eliminates the confounding effects that result from observational data (for example, between climate or edaphic factors that influence both SOC and yields). While other effects can also confound or obscure the SOC-to-yield relationship in this approach (for example, increases in both nitrogen availability and SOC from legume cover crops or increases in crop productivity that could also lead to SOC increases³²), building a broad yield model that examines possible confounders can increase confidence in the relationship between SOC and yield and its context dependence.

We use a global meta-analysis to determine how cover cropping affects SOC and crop yields simultaneously, and the extent to which changes in crop yield (Δ_{yield}) are related to changes in SOC (Δ_{SOC}). We thus build on previous meta-analyses that assess how cover cropping affects SOC or yields individually by linking these responses together in a paired treatment-control meta-dataset. We asked three questions. (1) Are co-benefits (simultaneous increases in crop yields and SOC) the most common response to cover cropping? (2) Do changes in SOC link directly to changes in yield, and if so, is this association related to nitrogen (N) inputs? (3) Regardless of direct links between SOC and yield, are there edaphic, environmental or management conditions where co-benefits of increased SOC and yield from cover cropping are more likely to be maximized? We compiled an exhaustive database of paired yield and SOC responses to cover cropping and constructed models with factors mediating their individual and joint responses. By building

Table 1 | Standardized coefficients and one-sided type III analysis of variance (ANOVA) results from our Δ_{yield} model ($n=417$)

Δ_{yield} model results			
Variable	Standardized coefficient	d.f.	P value
Initial SOC	0.01	1, 92	0.63
Δ_{SOC}	0.04	1, 43	0.06
Cover crop type	-0.14	1, 24	0.59
Rotational complexity	— ^a	2, 71	8.0×10^{-5}
N fertilizer	-0.13	1, 29	5.2×10^{-6}
Absolute latitude	-0.05	1, 88	0.09
$\Delta_{\text{SOC}} \times \text{initial SOC}$	-0.08	1, 71	0.004
Rotational complexity \times cover crop type	— ^a	2, 25	6.4×10^{-6}
N fertilizer \times cover crop type	0.17	1, 25	1.3×10^{-5}
$\Delta_{\text{SOC}} \times \text{cover crop type}$	-0.04	1, 32	0.16
$\Delta_{\text{SOC}} \times \text{N fertilization}$	0	1, 36	0.99

d.f., degrees of freedom for numerator and denominator, respectively, with Kenward–Roger approximation for denominator d.f.; Δ_{yield} , the log cash crop yield response ratio; Δ_{SOC} , the SOC change from cover cropping (g kg^{-1}); initial SOC, SOC (g kg^{-1}) before cover cropping; cover crop type, binary categorical: legume versus non-legume coded 1 and 0, respectively; N fertilization, in-season cash crop N fertilization ($\text{kg ha}^{-1} \text{ season}^{-1} \text{ N}$); rotational complexity, a categorical variable corresponding to the number of different cash crop species in rotation throughout the experiment. P values are considered significant at $\alpha=0.05$ ^aStandardized coefficient not presented for this categorical variable with multiple levels.

comprehensive models to identify and quantify important predictors of yield and SOC changes from cover cropping, our study not only helps identify farming systems most likely to see co-benefits from cover cropping but also informs policymakers seeking to quantify the impact of cropland carbon sequestration on global food production capacity.

Results

Joint impacts of cover cropping on crop yields and SOC

Our models, constructed from 434 paired observations spanning five continents (Supplementary Fig. 1), showed that cover cropping had a strong positive effect on both SOC and yield. The linear mixed-effect models, based on observations from all management types and sites, predicted yield and SOC changes of +10.9% (95% confidence interval (CI): 7.5–14.5) and +1.07 g kg^{-1} (95% CI: 0.82–1.32), respectively. The mean initial SOC concentration of our dataset was $15.5 \pm 9.2 \text{ g kg}^{-1}$ (\pm s.d.) at a mean sampling depth of $0\text{--}18.4 \text{ cm} \pm 7.3 \text{ cm}$ (\pm s.d.). Mean maize, rice and wheat yields (the three most common cash crops in the dataset) in control plots were 7.3 ± 4.0 , 3.7 ± 2.0 and $4.2 \pm 2.0 \text{ Mg ha}^{-1}$ (\pm s.d.). The mean experiment length (time from beginning of the experiment to sampling of SOC) was $7.7 \text{ yr} \pm 8.7$ (\pm s.d.).

In 59.7% of the 434 paired observations in our dataset, cover cropping increased both SOC and yields (Supplementary Fig. 2). Trade-offs, in which either SOC or yield increased while the other decreased, accounted for about one-third of observations. In 20.7% of paired comparisons, cover crops increased SOC but decreased yields; in 12.9% of cases, cover crops decreased SOC but increased yields. Co-costs, in which cover cropping negatively affected both yields and SOC, accounted for 6.7% of paired observations.

Explaining variability in crop yield responses to cover cropping

To help explain variation in crop yield responses to cover cropping and drivers underlying patterns of co-benefits and trade-offs, we considered 29 possible management and environmental variables as moderators (Supplementary Table 1). Significant predictors in our yield change

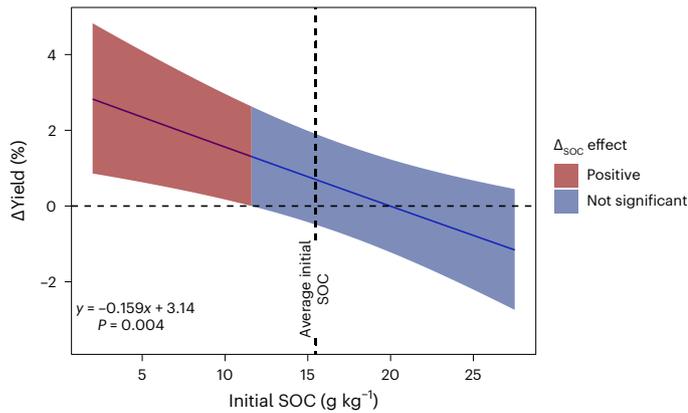


Fig. 1 | Relationship between changes in SOC and yield from cover cropping. Yield change associated with a +1 g kg⁻¹ increase in SOC (for example, from 5 g kg⁻¹ to 6 g kg⁻¹) at differing levels of initial SOC (blue centre line). Initial SOC is SOC (g kg⁻¹) before cover cropping (0–18.4 cm depth on average). Shaded bands are 95% CIs from two-sided *t* tests. Increased SOC is positively associated with yield (red) only in sites with below-average initial SOC (less than 11.6 g kg⁻¹). Overall, 90% of observations fell within the initial SOC range shown; 40 out of 92 study sites in our dataset had initial SOC levels below 11.6 g kg⁻¹.

(Δ_{Yield}) model included an interaction between SOC change (Δ_{SOC}) and initial SOC, in addition to rotational complexity and N fertilizer, with each of the latter two interacting with cover crop type (legume versus non-legume) (Table 1 and Supplementary Table 2). Marginal R^2 of our Δ_{Yield} model was 0.25, and conditional R^2 was 0.89, indicating unmeasured site-level effects accounted for a substantial proportion of variation. Addition of other variables such as soil texture, sampling depth or phosphorus inputs did not improve model fit (Supplementary Table 2). Addition of other variables for which we had complete data did not affect coefficient estimates of selected variables (Supplementary Table 6).

We found that SOC changes from cover cropping (Δ_{SOC}) were associated with yield changes (Δ_{Yield}), but only in soils with initial SOC values of 11.6 g kg⁻¹ or less (Fig. 1). In soils with initial SOC values of 5 g kg⁻¹, for example, a +1 g kg⁻¹ increase in SOC was associated with a +2.4% yield increase. In soils with initial SOC values greater than 11.6 g kg⁻¹, Δ_{SOC} was not significantly associated with Δ_{Yield} . The Δ_{SOC} -to- Δ_{Yield} relationship did not differ between cover crop types (legume versus non-legume) and did not vary across differing levels of N fertilization.

The effect of rotational complexity on Δ_{Yield} differed between legume cover crops and non-legume cover crops (Fig. 2b,c). Holding other predictors at their dataset average, Δ_{Yield} in legume cover crop treatments was significantly greater in continuous cash crop monocultures (+24.3%; 95% CI: 18.1–30.8) versus rotations with two (+11.0%; 95% CI: 3.1–19.5) cash crop species (Fig. 2b). For rotations with three or more cash crops, Δ_{Yield} from legume cover crops was not statistically different from zero. For non-legume cover crops, the magnitude of Δ_{Yield} varied across rotational complexity groups but not significantly so. Holding other predictors at their dataset average, non-legume cover crops significantly increased yield in continuous cash crop monocultures (+7.8%; 95% CI: 1.7–14.2) and in plots with three or more cash crops in rotation (+20.9%; 95% CI: 8.3–35.0) (Fig. 2c). Δ_{Yield} from non-legume cover crops in two-crop rotations was positive but overlapped zero (+7.2%; 95% CI: -0.8–15.9).

We found that increased N fertilization reduced Δ_{Yield} in legume cover crop treatments, but we did not find evidence of an N fertilization effect on Δ_{Yield} for non-legume cover crops (Fig. 2d,e). Legume cover crops in low-N systems (12.9 kg ha⁻¹ season⁻¹ N, one s.d. below the mean N fertilization of our dataset) increased yield by +20.4% (95% CI: 13.8–27.4) and in average-N systems (85.9 kg ha⁻¹ season⁻¹ N)

increased yield by +13.0% (95% CI: 7.0–19.3) (Fig. 2d). In systems receiving more than 157 kg ha⁻¹ season⁻¹ N (high N), we did not find evidence of yield changes from legume cover crops. Non-legume cover crops increased yields in low- (+9.5%; 95% CI: 2.9–16.6), average- (+11.8%; 95% CI: 5.2–18.7) and high- (+14.1%; 95% CI: 6.2–22.6) N systems (Fig. 2e).

SOC responses to cover cropping

Our Δ_{SOC} model included site-level aridity and an interaction between cover crop type (legume versus non-legume) and N fertilizer inputs (kg ha⁻¹ N) as variables that moderated the effect of cover crops on SOC (Table 2 and Fig. 3). Marginal R^2 was 0.15, and conditional R^2 was 0.82. Addition of other variables such as initial SOC, mean annual precipitation, phosphorus fertilization and tillage did not improve model fit (Supplementary Table 3). In line with the findings of ref. 11, we found that experiment duration (time since introduction of cover crops) was not a good predictor of SOC response.

We found that non-legume cover crops were less effective than legume cover crops at increasing SOC (+0.69 g kg⁻¹; 95% CI: 0.4–0.98 versus +1.37 g kg⁻¹; 95% CI: 1.11–1.63; Fig. 4d).

Cover crops were less effective at increasing SOC in more arid sites (Fig. 3c). For aridity values one s.d. above the dataset average, roughly in line with areas such as the southwestern US Corn Belt and Southern India, cover cropping increased SOC by +0.70 g kg⁻¹ (95% CI: 0.39–1.00) (Fig. 3c). For aridity values one s.d. below the dataset average, roughly in line with areas such as northern Japan and southwestern Brazil, cover crops increased SOC by +1.37 g kg⁻¹ (95% CI: 1.00–1.73).

Discussion

In our meta-analysis of 92 experiments spanning 5 continents, we found that cover crops increased crop yields concurrently with SOC in 59.7% of 434 paired observations, thus providing co-benefits for farmers and society a majority of the time. Δ_{SOC} was directly associated with Δ_{Yield} only in soils with relatively low SOC before cover cropping. The yield benefit of increased SOC did not diminish in systems with higher N inputs and did not differ between cover crop types (legume versus non-legume), indicating that N inputs cannot substitute for changes in SOC that link to higher yields. The largest SOC increases occurred in legume cover crop treatments (+1.5 g kg⁻¹), and the largest yield increases also occurred from legume cover crops in systems with low to average N inputs and in 1–2 crop rotations (up to +24.3%).

Direct relationships between changes in SOC and yield

As the source of carbon input to soil, photosynthesis is the most fundamental constraint on SOC sequestration³³. Cover cropping is considered one of the most promising approaches to increase SOC in agricultural soils, in part because it increases net primary productivity (NPP) relative to a bare fallow, and thus carbon inputs to soil^{33,34}. Cover cropping may also increase the carbon use efficiency of the soil microbial community³⁵, which determines the proportion of carbon inputs remaining in soil as microbial necromass, recognized as the primary source of stabilized soil carbon³⁶. However, since cover crops not only can help build SOC but also may increase crop productivity directly (in ways not mediated through changes in SOC), disentangling whether cover crops build SOC directly or build SOC through their effects on cash crop productivity is challenging³². In a supplemental model, we tested Δ_{Yield} as a predictor of Δ_{SOC} and did not find statistical evidence of an indirect effect of cover crops on Δ_{SOC} via changes in cash crop productivity (Δ_{Yield} was not a significant predictor of Δ_{SOC} and did not have a significant interaction with initial SOC, whereas Δ_{SOC} was a strong predictor of Δ_{Yield} in low-SOC soils) (Supplementary Table 8).

Further, the relative changes in NPP from increases in crop productivity versus cover cropping suggest that cover cropping is the dominant influence on SOC. In this study, if we assume half of above-ground cash crop biomass would be removed as yield³⁷, then the average increases in cash crop biomass returned to soil as residue for the three

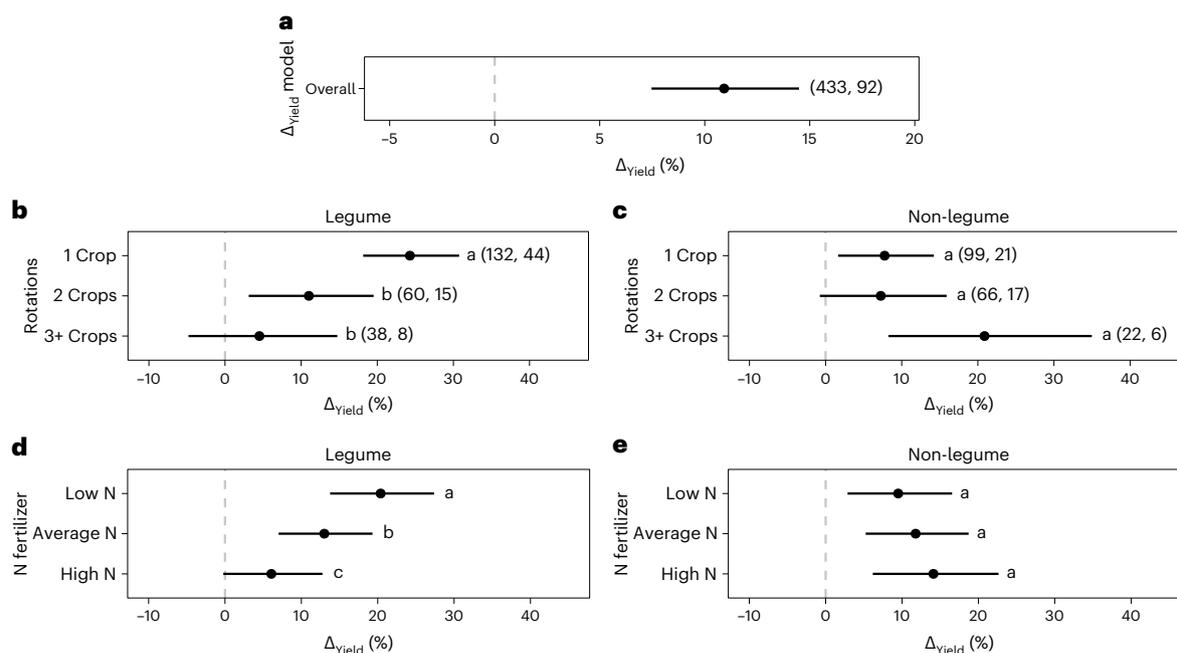


Fig. 2 | Moderators of cover cropping effects on cash crop yields. a–e, Cash crop yield change (Δ_{yield}) from cover cropping (**a**) at different levels of rotational complexity and (**b,c**) at differing levels of N fertilizer (**d,e**; $\text{kg ha}^{-1} \text{ season}^{-1}$ N) in our Δ_{yield} model ($n = 417$; $k = 88$). Selected N fertilizer levels are dataset mean \pm s.d. with low, average and high N corresponding to 12.9, 85.9 and 158.9 $\text{kg ha}^{-1} \text{ season}^{-1}$ N, respectively. Rotational complexity ('Rotations') is a count of the number of different cash crop species rotated on a given plot across the length of the experiment. Yield change estimates are shown for both legume (**b,d**) and

non-legume (**c,e**) cover crops. Letters are pairwise comparison results, with different letters indicating significantly different effect sizes at $\alpha = 0.05$ with Bonferroni adjustments for multiple comparisons. Numbers in parentheses are observations in each grouping followed by the number of unique sites in each grouping (not presented for N fertilizer because displayed estimates correspond to selected values along a continuous axis rather than groupings). Centre dots represent Δ_{yield} estimates. Error bars are 95% CIs.

Table 2 | Standardized coefficients and one-sided type III ANOVA results from our Δ_{SOC} model ($n = 418$; $k = 88$)

Δ_{SOC} model results			
Variable	Standardized coefficient	d.f.	P value
Cover crop type	-0.68	1, 32	3.0×10^{-5}
N fertilizer	-0.54	1, 64	0.003
Aridity	0.71	1, 71	0.004

d.f., degrees of freedom for numerator and denominator, respectively, with Kenward–Roger approximation for denominator d.f.; Δ_{SOC} , the measured cover crop treatment SOC concentration (g kg^{-1}) minus the measured SOC concentration of the paired control (g kg^{-1}); aridity, an index of site-level aridity (low numbers are more arid).

most common cash crops in the study were 0.9 (maize), 0.5 (rice) and 0.4 (wheat) Mg ha^{-1} . If crop residue were not retained, these values would be lower. Conversely, cover crop biomass of 3–7 $\text{Mg ha}^{-1} \text{ yr}^{-1}$ or higher is common¹¹ and consistent with the average increase of biomass on cover cropped plots in this study of 5.1 $\text{Mg ha}^{-1} \text{ yr}^{-1}$ ($n = 133$; $k = 47$), or 2.2 $\text{Mg ha}^{-1} \text{ yr}^{-1}$ for the difference between cover crop biomass and average weed biomass in fallow plots ($n = 49$; $k = 18$). With all of the cover crop biomass typically returned to the soil, this is -2.5–5.5 times greater biomass from cover crops directly than from changes to cash crop productivity. As opposed to the non-significant effect of absolute cash crop yield change on Δ_{SOC} ($P = 0.70$), the difference in cover crop biomass between treatment and control plots was a significant predictor of the absolute change in SOC ($P = 0.04$; $n = 49$; $k = 18$) (Supplementary Table 4). Thus, we conclude that cover crops directly increase SOC, with possible additional but smaller indirect (non-SOC mediated) effects from cash crop productivity.

Further, if yield increases from cover cropping were driving the positive $\Delta_{\text{SOC-to-}\Delta_{\text{yield}}}$ relationship, leading to higher SOC³², then this mechanism should increase SOC in soils regardless of initial SOC level, especially since the Δ_{SOC} model showed no signs of SOC saturation in soils with higher initial SOC concentrations (initial SOC was not a predictor of Δ_{SOC}). The best explanation for this interaction is that the smaller $\Delta_{\text{SOC-to-}\Delta_{\text{yield}}}$ response in higher SOC soils is a reflection of decreasing marginal yield benefits from increased SOC in higher-initial-SOC soils.

Our experimentally based approach identified a $\Delta_{\text{SOC-to-}\Delta_{\text{yield}}}$ response that does not vary on the basis of N inputs or with legume versus non-legume cover crops, as indicated by the lack of significant interactions between Δ_{SOC} and these predictors. A negative Δ_{SOC} by N fertilization interaction would have indicated that the yield benefit from SOC was substitutable for N inputs and therefore N related. Likewise, if the $\Delta_{\text{SOC-to-}\Delta_{\text{yield}}}$ relationship differed between legume and non-legume cover crops, then some portion of the SOC benefit probably would have been a reflection of yield benefits from N fixation. In the absence of these interactions with Δ_{SOC} , the link we found between Δ_{SOC} and Δ_{yield} is probably better explained by benefits of increased SOC such as reduced compaction and increased aeration³. Our results thus help to identify and quantify the yield benefits of soil improvement provided by SOC for which fertilization cannot substitute.

We found marginal yield increases from changes in SOC only when SOC before cover cropping was less than 11.6 g kg^{-1} , which helps clarify contradictory results of previous observational meta-analyses. For example, in a meta-analysis of Danish farms showing no relationship between yield and SOC²⁶, there were very few observations with SOC concentrations below 11.6 g kg^{-1} . Contrastingly, a study from China reported positive and linear relationships between yield and SOC²⁸, but had few observations over -15 g kg^{-1} . Only a global meta-analysis

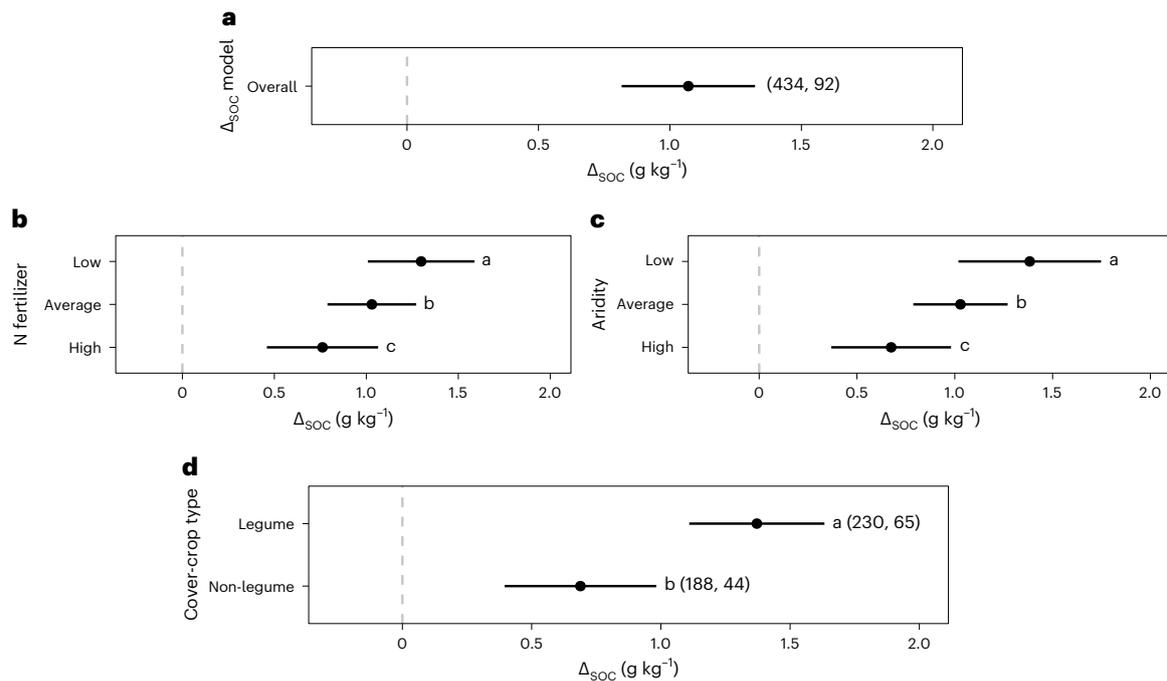


Fig. 3 | Moderators of cover cropping effects on soil organic carbon. **a–d**, Overall Δ_{SOC} (g kg^{-1}) in our Δ_{SOC} model (**a**), across differing levels of N fertilizer (**b**), at selected values of site-level aridity (**c**; ‘Aridity’) and between cover crop types (**d**; legume versus non-legume). Selected N fertilizer levels are dataset mean \pm s.d. with low, average and high N corresponding to 12.9, 85.9 and 158.9 kg ha^{-1} season $^{-1}$ N, respectively. Selected aridity levels are dataset mean \pm s.d. Cover crop type is binary categorical, non-legume versus legume.

Letters are pairwise comparison results, with different letters indicating significantly different effect sizes at $\alpha = 0.05$ with Bonferroni adjustments for multiple comparisons. Numbers in parentheses are observations in each grouping followed by the number of unique sites in each grouping (not presented for N fertilizer and aridity because displayed estimates correspond to selected values along a continuous axis rather than groupings). Centre dots represent Δ_{SOC} estimates. Error bars are 95% CIs.

which had a similarly wide range of SOC values as this study⁵ showed a saturating yield benefit similar to ours. The yield benefit of increased SOC that we identified is slightly less than that reported in the latter study. For a hypothetical increase in SOC from 5 g kg^{-1} to 8 g kg^{-1} , our model predicted a +7.9% yield increase, compared with the +10% yield increase previously reported⁵. An SOC increase of this size takes many years of improved management; as an example, with assumptions of bulk density equal to 1.3 g cm^{-3} and the average carbon sequestration rate from cover cropping reported in ref. 13 of 0.32 $\text{MgC ha}^{-1} \text{yr}^{-1}$ (to a mean soil depth of 22 cm), a change from 5 g kg^{-1} to 8 g kg^{-1} SOC would take ~27 years.

Aligning carbon sequestration goals with yield benefits

Regardless of *direct* links between Δ_{SOC} and Δ_{Yield} , we found that incorporation of legume cover crops into systems with one to two cash crops in rotation could build SOC while also increasing crop yields. These co-benefits occurred regardless of initial SOC concentration. Legume cover crops provided increases of +1.5 g kg^{-1} SOC and +24.3% yield in continuous monocrop cultures. In two-crop rotations, legume cover crops increased yield by +11.0% while the +1.5 g kg^{-1} SOC increase remained unchanged (we did not find evidence for crop rotation moderating Δ_{SOC}). Yield benefits of crop rotation diversification are well known^{38,39} and, judging from our results here, appear to be redundant with legume cover crops in more complex rotational systems. This suggests a need for further research on how to optimize cover crops in more complex cash crop rotations, for example, with mixes of cover crop species⁴⁰.

We identified low- to average-N-input systems as other key farm types where cover crops support alignment between carbon sequestration goals and yield increases. Effects of cover crops on SOC declined as N inputs increased, and yield benefits from legumes were highest in

low-N-input systems. Legumes could thus allow for increasing yields while keeping synthetic N fertilizer inputs low or even reducing them⁴¹, which also comes with environmental benefits. When legume cover crops are introduced, reducing N fertilizer inputs would help counter-balance possible increases in nitrous oxide emissions that can occur in legume systems^{42,43}.

The larger SOC response from legume compared with non-legume cover crops (+1.37 g kg^{-1} versus +0.69 g kg^{-1}) contrasts with previous meta-analyses that found no difference in SOC response between legume and non-legume cover crops^{11,13}, possibly due to their more limited datasets. With relatively more labile plant inputs that microbes efficiently use, legumes may be particularly effective at building soil organic matter pools, including mineral-associated organic matter, that both are relatively stable and supply N^{35,44–46}. Greater absolute changes in SOC in less-arid climates may be due to higher cover crop NPP. While aridity was not in our final Δ_{Yield} model, other studies show cover cropping leads to higher cash crop yields in less-arid climates^{18,47}, suggesting that such areas may be most likely to have co-benefits for SOC and yields.

Synthesis of research-station experimental trials, such as this study, has been the most common approach to understanding the yield effects of cover cropping^{16,17,19}, with less information available from working farms. Ref. 20 used satellite observations of yields and adoption of cover cropping on farmers’ fields across six states in the US Midwest, showing small maize and soybean yield declines following cover cropping. Observations of yield declines could be due in part to the predominant use of non-legume cover crops in two-cash-crop rotations in this region²⁰, which our meta-analysis showed having negligible yield benefits (Fig. 2c). Given the importance of cover crop type to yield (and SOC) outcomes, remote-sensing studies that differentiate cover crop functional types are needed. Fusing data from experimental trials

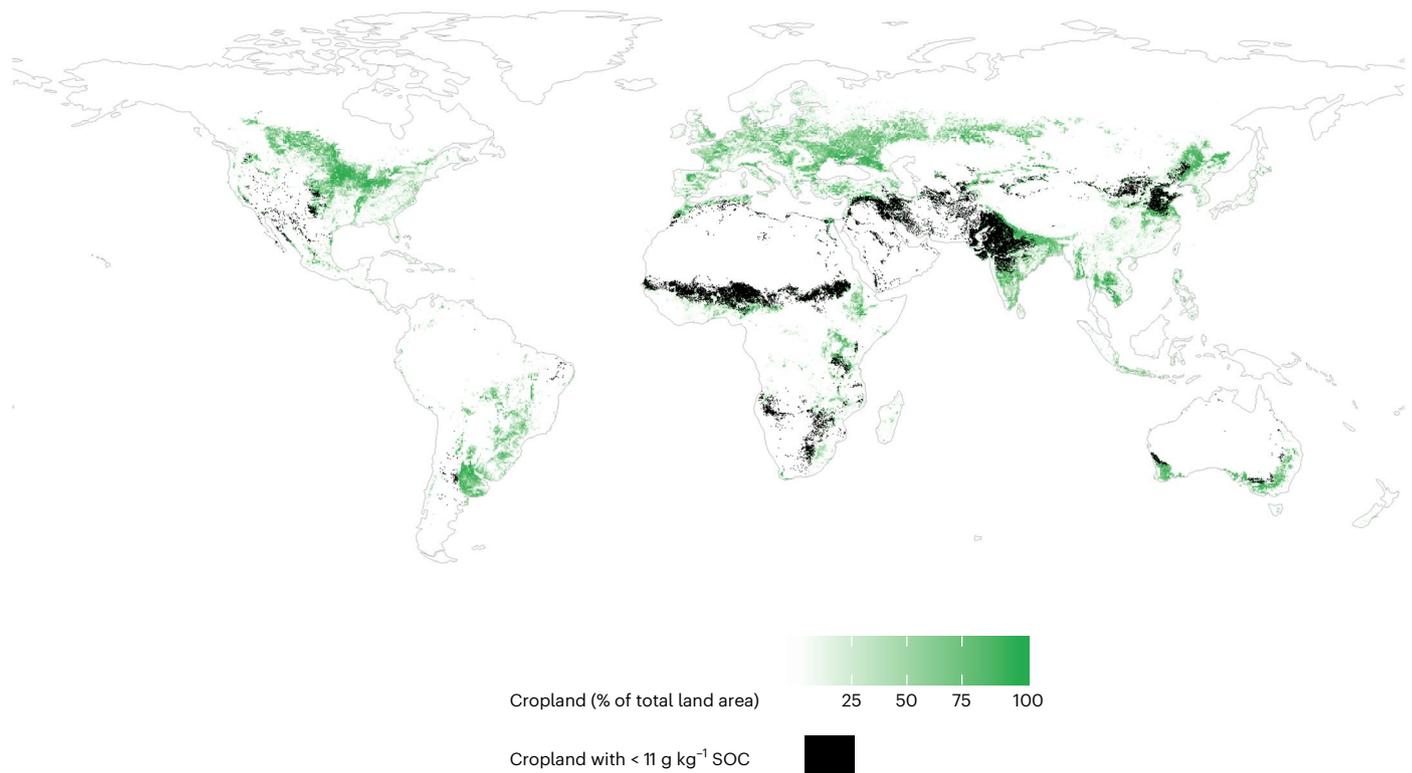


Fig. 4 | Overlap between global cropland and soils with SOC values < 11 kg⁻¹. Global cropland in 2019 (Global Land Analysis & Discovery⁶⁶) with 0–15 cm SOC concentrations < 11 g kg⁻¹ highlighted in black (weighted mean of 0–5 and 5–15 cm depths; SoilGrids⁶⁷). Continent borders are outlined in light grey using

a World Geodetic System 1984 projection. The SOC concentration data are mapped at 1 km resolution. Global cropland extent is mapped at 3 km resolution and consists of all herbaceous food, forage (excluding permanent pastures) and biofuel crops⁶⁶. See Supplementary Methods for detailed methods.

and satellite observations may be the best route for understanding impacts of cover cropping in real-world contexts⁴⁸.

Our global meta-analysis demonstrates that the goal of building soil carbon through cover cropping aligns with the goal of increasing or maintaining crop yields. Importantly, since these goals align at the site level ~60% of the time, benefits of higher yields for farmers are achievable concurrently with the societal benefit of carbon sequestration¹⁰. Yield benefits related to increases in SOC were evident only in soils with initial SOC concentrations below 11.6 g kg⁻¹ (43.4% of studies in our dataset). This finding suggests that direct yield benefits from SOC increases could help motivate farmers' adoption of SOC-enhancing practices in soils with low SOC. Globally, approximately 14% of cropland has SOC concentrations in the 0–15 cm depth of 11 g kg⁻¹ or lower (Fig. 4). SOC accrual could help improve productivity on more than ~27 Mha of maize and wheat cropland that are producing below-potential yield on land predicted to have less than 11 g kg⁻¹ SOC (Supplementary Fig. 4 and Supplementary Table 5). While this number should be cautiously interpreted as the absolute technical potential (in terms of applicable land area) for direct yield benefits from SOC accrual, other co-benefits of cover cropping for SOC and yields (those not driven by direct SOC effects on yield) will be more widespread. Bounding the global potential for cover cropping co-benefits will require consideration of constraints such as short growing seasons and low water availability that limit cover crop adoption¹⁸ and SOC accrual, as well as increasing data availability from regions not well represented in our dataset (for example, eastern and southern Africa).

We therefore suggest that determining the context-specific conditions for which changes to agricultural management provide co-benefits for crop yields and SOC—rather than establishing universal relationships between SOC and yield—will be more useful for spurring

agricultural transitions that produce food while also sequestering carbon. To achieve carbon sequestration goals while supporting crop yields, diversifying simplified rotations with legumes is a promising strategy given that legumes often provided the largest benefit to both SOC and yields. Likewise, in low- to average-N-input systems, the greatest yield benefits can be aligned with the greatest SOC benefits through the use of legume cover crops. For systems with complex rotations or high N inputs, non-legume cover crops are a better choice to support yield goals, although SOC changes may be lower. Identifying when and where agricultural management practices that build SOC also deliver direct benefits to farmers will support the urgent need to increase the carbon sink of agricultural lands.

Methods

Study selection

We selected cover cropping studies according to the following criteria: (1) the experimental design includes one or more replicated cover cropping treatments, defined as a non-harvested crop grown between productive seasons; (2) the study includes a clear control as either bare fallow or spontaneous off-season regrowth (for example, 'winter weeds'); (3) data are available for both SOC and cash crop yield, each measured no more than one year apart; (4) cash crop yield is measured as fruit or grain; (5) yield and SOC are available as yearly or monthly values rather than averages across multiple years (for maximum accuracy in matching SOC values with associated yields); and (6) annual fertilizer inputs are equal across control and treatment or are administered on the basis of pre-season soil tests. Potted-plant experiments were not included in our dataset.

We began our literature search with the study lists of two recent cover cropping meta-analyses^{13,17} and subsequently searched Institute for Scientific Information Web of Science for additional studies that

matched our criteria using the search string TS = ((cover crop* OR catch crop OR fallow OR green manure) AND carbon AND yield). In October 2020, the date of our final search, our search string returned 2,451 studies. If an article reported only SOC data or yield data, we used key terms related to the experiment to search Google Scholar for articles reporting on the same experiment to fill in the missing data. In 11 instances, grey literature sources such as master's theses, dissertations and conference proceedings were used to supplement data from peer-reviewed publications. In addition to Google Scholar searches, 36 authors were contacted for additional data or methodological clarifications, out of which 8 responded and 3 provided additional data and/or information.

Our final dataset spanned 5 continents and contained data from 92 distinct experiments gathered from 120 sources (107 peer-reviewed journal articles, 6 master's theses, 2 dissertations, 3 publicly available datasets and 2 conference proceedings). A list of data sources used in our study along with extraction notes are provided as Supplementary Information files for reproducibility.

Data compilation and extraction

We quantified the effect of cover crops on yield using the log response ratio, calculated as the natural log of the cover crop treatment value divided by that of the respective fallow control. For SOC, we used the absolute difference in SOC concentration between the cover crop and control plots, which allowed us to assess the influence of initial SOC without the possibility of statistical artefacts associated with relative differences⁴⁹. Within a given study, a treatment value was matched to a control value only if both groups differed in no other respect than the use of cover cropping (for example, same tillage regime, same N application and so on) and if the treatments were sampled at the same time. This aspect of our study design allowed us to control for confounding effects that would otherwise be introduced in a direct comparison of raw values between studies such as environmental conditions, management decisions or edaphic factors. In the case of the yield response to cover cropping, our use of the response ratio allowed us to make comparisons across crops with different morphological characteristics (for example, tomatoes versus cotton) because weight units are normalized by the ratio. Site-level initial SOC values were not available for some of the studies in our dataset. To approximate missing site-level values, we used the earliest SOC sample available for the non-cover-crop control, assuming that the field had probably been under a no-cover-crop planting regime before the initiation of the cover cropping experiment. We combined soil metrics and variance measures reported from multiple depths into one single depth using a weighted average that accounted for the size of each depth increment relative to the total depth sampled. Supplementary Fig. 9 shows a histogram of deepest sampling depth. In our model selection process, we assessed the impact of sampling depth as a moderating factor of the effect of SOC on yield. Although differing sampling depths across studies have the potential to obscure trends when comparing raw SOC values, we did not find that sampling depth was a significant predictor of initial SOC values in our dataset. We therefore opted to test initial SOC effects using raw SOC values.

Data analysis

We collected sampling variances when available to assign weights to data points. However, only 30% of studies reported some form of variance. Following previous work, we chose instead to weight our observations using sample size of the treatment and control groups, which gave more weight to larger, well-replicated studies^{50–52}. Our weighting formula (equation (1)) includes the common weighting ratio based on treatment-group sample size (n_t) and control-group sample size (n_c) as well as a correction term dividing by the total number of observations contributed by a given study (N). This additional step is meant to ensure that no study contributes a disproportionate amount

to the final model simply because it contained more extractable data points than another⁵³.

$$W = \frac{n_t \times n_c}{n_t + n_c} \times \frac{1}{N} \quad (1)$$

We modelled study site as a random effect to account for the non-independence of these data points and nested sampling year within study site to account for temporal non-independence.

The primary goals of our analysis were to assess the relative importance of soil, management and climate factors expected to affect Δ_{Yield} and Δ_{SOC} and to quantify the relationship between Δ_{Yield} and Δ_{SOC} while taking these factors into account. We obtained 29 possible variables that were readily available from published studies (Supplementary Table 1). All of these variables are known to affect SOC and yields. We used a two-step process, first using model selection to identify predictor variables most strongly associated with Δ_{Yield} or Δ_{SOC} response variables, and second verifying that variables not selected did not affect coefficient estimates or significance of selected variables. To build models for both Δ_{SOC} and Δ_{Yield} , we used Akaike information criterion (AIC)⁵⁴ scores to select variables that we had hypothesized may be mechanistically related to Δ_{SOC} or Δ_{Yield} . While risks of model selection for causal interpretation (as opposed to prediction) have recently been highlighted^{55,56}, a two-step process allowed us to home in on the predictor variables that account for the most variation in the responses and then ensure that coefficient estimates are robust in the second step. Variable relevance was determined by comparing weighted mixed-effect models of each variable as a solitary predictor of each response variable against the corresponding model containing only the intercept. Because of incomplete data for certain predictor variables, model comparisons between the solitary predictor and the intercept-only model were done using complete data subsets for the solitary predictor. If the regression containing the solitary predictor variable resulted in an AIC score more than two units below that of the intercept-only regression ($\Delta\text{AIC} < 2$), the variable was included in our final multiple regression model. We did not perform any further model selection because complex model selection decisions are often subjective and can change results considerably⁵⁷.

Given the variables in our model, there were a number of possible interactions. We tested specific interactions on the basis of questions we wanted to explore concerning the relationships among Δ_{Yield} , Δ_{SOC} , soil properties and management factors. For our Δ_{Yield} model, we tested interaction terms between Δ_{SOC} and soil texture metrics, as well as an interaction between Δ_{SOC} and initial SOC (SOC concentration before cover cropping). Our hypothesis was that the effect of changes in SOC concentrations from cover cropping would depend on how much SOC was present, as per previous findings⁵. We also tested interaction terms between cover crop type (legume versus non-legume) and yield predictor variables whose effects we hypothesized may be influenced by N fixation such as N fertilization, rotational complexity and Δ_{SOC} . To test whether increases in cash crop productivity from non-SOC-related cover cropping benefits were responsible for increases in SOC, rather than increases in SOC being responsible for increases in yields, we included Δ_{Yield} as a possible predictor of Δ_{SOC} in our Δ_{SOC} model. We also tested an interaction term between Δ_{Yield} and initial SOC in our Δ_{SOC} model.

In both models, we checked for collinearity among variables using generalized variance inflation factors (GVIF) with the following adjustment to allow for comparability across variables with differing degrees of freedom⁵⁸ (d.f.): Adjusted GVIF = (GVIF)^{2/d.f.}. We considered adjusted GVIF values of 3 and higher to indicate potential collinearity⁵⁹. The only cases of collinearity involved models that included annual temperature and precipitation and the aridity index. These variables were assessed separately in regression models and the final variable chosen on the basis of AIC. We centred predictors so that 0 corresponded with the

observed mean of each predictor by subtracting the dataset mean from each observation and subsequently standardized coefficients by dividing by two standard deviations⁶⁰. In our Δ_{yield} model, cover crop type was coded as 1 (non-legume) or 0 (legume) to allow for comparison of standardized coefficients⁶⁰.

To ensure that the selected models were robust, in the second step we added back in all possible predictor variables for which we had data for all observations, for both the Δ_{yield} and Δ_{SOC} models. In this step, we showed that parameter estimates were insensitive to these additional controls, which helps allow for causal statistical inference by showing that variation in the data is not misallocated across the focal predictor variables because of omitted variables⁵⁵. We report coefficients from these larger models in Supplementary Tables 7 and 8.

To explore, from an NPP perspective, whether changes in cash crop yield from cover cropping were driving changes in SOC versus changes in SOC from cover cropping driving changes in yield, we built three separate weighted mixed-effect regressions for Δ_{SOC} (Supplementary Table 4). We tested cover crop above-ground biomass as a solitary predictor of Δ_{SOC} and subsequently cover crop above-ground biomass difference (cover crop above-ground biomass minus above-ground biomass of spontaneous off-season regrowth in control plots when these data were available) as a solitary predictor of Δ_{SOC} . Finally, we tested absolute cash crop yield change (the measured cash crop yield of the cover crop treatment in Mg ha^{-1} minus the measured cash crop yield of the paired fallow control (Mg ha^{-1})) as a solitary predictor of Δ_{SOC} . For absolute cash crop yield change, only crops with yields reported in constant dry weight and with harvest indexes of approximately 0.5 were included since absolute yields of these crops are comparable (for example, versus tomatoes, with yields reported in wet weight) as a proxy for total above-ground biomass.

All analyses were performed using R Statistical Software v.4.2.0⁶¹. We built mixed-effect regressions using the package lme4⁶² and determined fixed-effect F values using a type III analysis of variance in the stats package⁶¹. We used the package emmeans to quantify interaction effects⁶³. We used pairwise comparison in the package emmeans to determine significant differences among levels of categorical variables using $\alpha = 0.05$ with a Bonferroni adjustment for multiple comparisons⁶⁴. To determine the significance of different levels of our moderating factors, we checked to see whether their 95% CI overlapped zero, with no overlap indicating a rejection of the null (zero effect) at $\alpha = 0.05$. When reporting response estimates at specific values of predictor variables, we held all other predictor variables at their dataset average. We used the Kenward–Roger approximation for denominator degrees of freedom in all P -value calculations⁶⁵.

Assessing bias and outliers

Using the InfluencePlot function in the car package⁷, we identified highly influential data points using Cook's distance and assessed the impact of their removal on our models to gauge robustness to extreme data points. Starting from the full dataset, we sequentially removed the point with the highest Cook's distance in each model and re-ran the models on each trimmed dataset. Using ten sets of results for each model, each subsequent one with an additional influential point removed, we compared changes in effect-size coefficients and P values to determine whether any were highly influenced by one observation (see Supplementary Table 1 for full comparison results). We noted one such observation that caused the effect of tillage type on Δ_{yield} to be highly significant. Upon removal of this observation, this effect became non-significant, and successive removal of influential points after this produced stable effect-size estimates (Supplementary Table 4). As such, we chose to remove this outlier from our Δ_{yield} model to report robust results that reflected the dominant trends in our dataset. In addition to influential data-point removal, we conducted a leave-one-out sensitivity analysis in which we removed studies from

our dataset one study at a time and recalculated coefficient estimates on each trimmed dataset. After performing this removal for all 92 studies in both our Δ_{SOC} and Δ_{yield} models, we assessed the variability in coefficient estimates among trimmed datasets (Supplementary Figs. 5 and 6) and looked for outlier estimates that would have indicated that one study was having an outsized effect on model fit. In addition, we looked at each leave-one-out model that pushed coefficient estimates for significant predictors towards the null (0) and away from the null (0) for non-significant predictors to see whether the significance of any given predictor was dependent on a single study or whether the non-significance of any given predictor was dependent on a single study (either of which would be a sign of unstable coefficient estimates). We found that variability in all coefficient estimates was low and that significance or non-significance of any given predictor was not dependent on any given study. We looked for publication bias in our dataset on both the yield and SOC response ratios using funnel plots (Supplementary Fig. 3).

Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

Data availability

Data used in this meta-analysis are publicly available from the Dryad Digital Repository: <https://doi.org/10.6078/D1013R>. Global yield gap data in Fig. 4 were used from the Global Yield Gap Atlas8 (www.yieldgap.org).

Code availability

Code used in this meta-analysis are publicly available from the Dryad Digital Repository: <https://doi.org/10.6078/D1013R>.

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Author contributions

I.V., T.M.B. and L.P. conceived the ideas and designed methodology; I.V. and G.D.L.C. collected the data; I.V., A.G., K.E., and A.C.M. analysed the data; I.V. and T.M.B. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Competing interests

The authors declare no competing interests.

Additional information

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Software and code

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Data collection No software was used during data collection for this study.

Data analysis All data analysis was undertaken in R version 4.2.0, using existing packages and functions. Specific packages (version #) used include lme4 (1.1-29), emmeans (1.7.3), stats (4.2.0), car (3.0-12), and terra (1.7-18)

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All manuscripts must include a [data availability statement](#). This statement should provide the following information, where applicable:

- Accession codes, unique identifiers, or web links for publicly available datasets
- A list of figures that have associated raw data
- A description of any restrictions on data availability

Data used in this meta-analysis are publicly available from the Dryad Digital Repository, accession <https://doi.org/10.6078/D1013R>. Global yield gap data in Fig. 4 was used from the Global Yield Gap Atlas8 (www.yieldgap.org)

Field-specific reporting

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Life sciences Behavioural & social sciences Ecological, evolutionary & environmental sciences

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Ecological, evolutionary & environmental sciences study design

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Study description	This study used meta-analysis of data from field experiments comparing cover cropping with fallow treatments to investigate effects of cover cropping on cash crop yields and soil organic carbon. Our final dataset spanned 5 continents and contained data from 82 distinct experiments gathered from 120 sources (107 peer reviewed journal articles, 6 master's theses, 2 dissertations, 3 publicly available datasets, and 2 conference proceedings). A list of data sources used in the study along with extraction notes is provided in the supplementary material.
Research sample	We selected cover cropping studies according to the following criteria: 1) the experimental design includes one or more replicated cover cropping treatments, defined as a non-harvested crop grown between productive seasons; 2) the study includes a clear control as either bare fallow or spontaneous off-season regrowth (e.g., "winter weeds"); 3) data are available for both SOC and cash crop yield, each measured no more than one year apart; 4) cash crop yield is measured as fruit or grain; 5) yield and SOC are available as yearly or monthly values rather than averages across multiple years (for maximum accuracy in matching SOC values with associated yields); and 6) annual fertilizer inputs are equal across control and treatment or are administered based on pre-season soil tests. Potted plant experiments were not included in our dataset. We began our literature search with the study lists of two recent cover cropping meta-analyses and subsequently searched ISI Web of Science for additional studies that matched our criteria using the search string TS=((cover crop* OR catch crop OR fallow OR green manure) AND carbon AND yield). In October 2020, the date of our final search, our search string returned 2,451 studies.
Sampling strategy	Data for this study were collected from previously published studies. Any study meeting the criteria described in "research sample" were included, providing a comprehensive assessment of all available literature.
Data collection	Data were extracted from published studies, including information on cash crop yields and soil organic carbon, as well as 29 moderator variables that are defined in the supplement. Data were extracted by the lead author (I.V.), along with independent extraction of approximately half of the data by co-author G.D.L.C. in order to identify any issues with the reliability of data extraction. No issues were found.
Timing and spatial scale	The final date of our search was October 2020, so any study from anywhere in the world meeting all criteria that was published prior to that date was included.
Data exclusions	Using the 'InfluencePlot' function in the 'car' package, we identified highly influential data points using Cook's distance and assessed the impact of their removal on our models to gauge robustness to extreme data points. Starting from the full dataset, we sequentially removed the point with the highest Cook's distance in each model and re-ran the models on each trimmed dataset. Using 10 sets of results for each model, each subsequent one with an additional influential point removed, we compared changes in effect size coefficients and p-values to determine if any were highly influenced by one observation (see Table S1 for full comparison results). We noted one such observation which caused the effect of tillage type on Δ Yield to be highly significant. Upon removal of this observation, this effect became non-significant and successive removal of influential points after this produced stable effect size estimates (Table S4). As such, we chose to remove this outlier from our Δ Yield model to report robust results which reflected the dominant trends in our dataset.
Reproducibility	All the studies included in this meta-analysis have already been published. Search terms and selection criteria for included studies were carefully documented. Results of the model selection process are presented in the supplement.
Randomization	The underlying data included in this meta-analysis were based on field experiments involving a variety of experimental designs. We defined a list of possible covariates that could moderate the impact of cover cropping on crop yield and soil carbon, or the relationship between the two, a priori and comprehensively assessed their impact on the yield and soil organic carbon response ratios.
Blinding	Blinding was not necessary as none of the data used in this study was subjective nor could be influenced by researcher biases.
Did the study involve field work?	<input type="checkbox"/> Yes <input checked="" type="checkbox"/> No

Reporting for specific materials, systems and methods

We request information from authors about some types of materials, experimental systems and methods used in many studies. Here, indicate whether each material, system or method listed is relevant to your study. If you are not sure if a list item applies to your research, read the appropriate section before selecting a response.

Materials & experimental systems

n/a	Involvement in the study
<input checked="" type="checkbox"/>	<input type="checkbox"/> Antibodies
<input checked="" type="checkbox"/>	<input type="checkbox"/> Eukaryotic cell lines
<input checked="" type="checkbox"/>	<input type="checkbox"/> Palaeontology and archaeology
<input checked="" type="checkbox"/>	<input type="checkbox"/> Animals and other organisms
<input checked="" type="checkbox"/>	<input type="checkbox"/> Human research participants
<input checked="" type="checkbox"/>	<input type="checkbox"/> Clinical data
<input checked="" type="checkbox"/>	<input type="checkbox"/> Dual use research of concern

Methods

n/a	Involvement in the study
<input checked="" type="checkbox"/>	<input type="checkbox"/> ChIP-seq
<input checked="" type="checkbox"/>	<input type="checkbox"/> Flow cytometry
<input checked="" type="checkbox"/>	<input type="checkbox"/> MRI-based neuroimaging