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Enhancing Soil Organic Matter as a Route to the Ecological Intensification of European Arable Systems

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ABSTRACT

Soil organic matter (SOM) is declining in most agricultural ecosystems, impacting multiple ecosystem services including erosion and flood prevention, climate and greenhouse gas regulation as well as other services that underpin crop production, such as nutrient cycling and pest control. Ecological intensification aims to enhance crop productivity by including regulating and supporting ecosystem service management into agricultural practices. We investigate the potential for increased SOM to support the ecological intensification of arable systems by reducing the need for

nitrogen fertiliser application and pest control. Using a large-scale European field trial implemented across 84 fields in 5 countries, we tested whether increased SOM (using soil organic carbon as a proxy) helps recover yield in the absence of conventional nitrogen fertiliser and whether this also supports crops less favourable to key aphid pests. Greater SOM increased yield by 10%, but did not offset nitrogen fertiliser application entirely, which improved yield by 30%. Crop pest responses depended on species: *Metopolophium dirhodum* were more abundant in fertilised plots with high crop biomass, and although population growth rates of *Sitobion avenae* were enhanced by nitrogen fertiliser application in a cage trial, field populations were not affected. We conclude that under increased SOM and reduced fertiliser application, pest pressure can be reduced, while partially compensating for yield deficits linked to fertiliser reduction. If the benefits of reduced fertiliser application and increased SOM are considered in a wider environmental context, then a yield cost may become acceptable. Maintaining or increasing SOM is critical for achieving ecological intensification of European cereal production.

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Key words: aphids; ecological intensification; fertiliser, soil organic matter; arable farming.

INTRODUCTION

Developing agricultural systems less dependent on unsustainable inputs, yet meeting the needs of a growing population, is a key challenge for food production systems in the future (Garnett and others 2013). Taking an ecosystem approach to agricultural food production is the goal of ecological intensification, which aims to enhance crop productivity by including regulating and supporting ecosystem service management into agricultural practices to reduce reliance on unsustainable inputs such as mineral fertiliser and pesticides (Bommarco and others 2013). A number of these ecosystem services including pollination by insects and crop pest regulation by natural enemies are supported by natural habitats located in the agricultural landscape, and it is at this scale that they need to be protected and managed to promote ecological intensification (Tscharntke and others 2005; Power 2010). Additionally, management at the field scale is key to effective ecological intensification. For example, soil organic matter decline, and the loss of the functionally important soil organisms it supports, is a major threat to the sustainability of agricultural systems (Gardi and others 2013; Tsiafouli and others 2015). Soil biodiversity loss can compromise key processes that deliver ecosystem goods and services on which effective ecological intensification relies, including decomposition and nutrient cycling (Lavelle and others 2006; Barrios 2007). Ecologically intensive practices include increased crop diversification, legumes in a rotation, application of organic fertilisers and minimising soil disturbance (Drinkwater and others 1998; Edmeades 2003; Kremen and Miles 2012). These may increase soil organic matter (SOM) and the biodiversity-based belowground ecosystem services it supports to enhance sustainability of agricultural systems and maintain or improve crop yields (Lal 2006; Barrios 2007; Brady and others 2015).

Not only does retaining high soil organic matter affect nutrient availability and growth of crop plants, but soils can also have direct or indirect resource-based (bottom-up) effects on crop pests through a variety of mechanisms. High organic matter content in soil can support a greater diversity of soil organisms, which provide alternative food sources for natural enemies that help to sup-

press crop pests (Scheu 2001; Birkhofer and others 2008). In addition, the 'mineral balance hypothesis' proposed by Phelan and others (1996) states that the balance of nutrients often found in organically managed soils promotes optimum conditions for plant growth, prevents pulses of available nutrients in plant tissues and reduces palatability or preference by pests (Altieri and Nicholls 2003; Alyokhin and others 2005). Accordingly, increases in soil organic matter may not only promote high soil organism abundance and diversity, but also lower pest pressure on crops.

In conventional, intensive agriculture, crop pests generally benefit from the application of fertilisers (Garratt and others 2011; Butler and others 2012). One group of insect herbivores especially responsive to fertiliser application are aphids. Cereal aphids, including the rose-grain aphid (*Metopolophium dirhodum*), the grain aphid (*Sitobion avenae*) and the bird cherry-oat aphid (*Rhopalosiphum padi*), are key pests of European cereal production causing direct feeding damage and virus transmission (Blackman and Eastop 2000). Furthermore, their pest status could increase in the coming decades under the influence of a changing climate (Sheppard and others 2016), reduced capacity to control them using chemical means due to developing resistance (Foster and others 2014), or following further insecticide restrictions amid concerns over environmental risks (Chagnon and others 2015). The positive response shown by aphids to nitrogen fertiliser in particular is thought to be due to the improved nutritional quality of the host plant amino acid profile (Weibull 1987; Awmack and Leather 2002), which can promote aphid growth and fecundity (Ponder and others 2000; Khan and Port 2008). Indirect effects of soil fertility on cereal aphids, mediated through effects on host morphology and attractiveness, are also apparent (Honěk and Martinková 2002; Garratt and others 2010b). Therefore, fertiliser application can result in higher population densities of cereal aphids (Hasken and Poehling 1995; Wang and others 2015; Zhao and others 2015) with consequent effects on crop damage, virus transmission and yields (van Emden and Harrington 2017). Given the importance of aphids as pests to European cereal production, promoting agricultural practices that maintain or improve crop yield while reducing pest pressure will support long-term sustainable pro-

duction which is less reliant on chemical pest control.

Ecological intensification involves making better use of regulating and supporting ecosystem services in agricultural systems. As a result, crop production is maximised while environmental impacts to the wider ecosystem are minimised through the decrease, but not necessarily exclusion, of anthropogenic inputs (Bommarco and others 2013). Given the potential impacts of managing SOM and fertiliser application on yield and pest control, an integrated approach to soil fertility management taking into account ecosystem services could be a significant step towards ecological intensification of cereal production in Europe. Therefore, it is important to assess how current declines in SOM and intensive fertiliser application affect both crop production and key pests.

The aim of this study was to investigate the potential for increased SOM to support the ecological intensification of arable systems by reducing the need for nitrogen fertiliser application and pest control. Using a large-scale European field trial implemented across 84 fields in 5 countries, we tested whether increased SOM (using soil organic carbon as a proxy) helps recover yield in the absence of conventional nitrogen fertiliser application by promoting reproductive rather than vegetative crop growth and improving harvest index, and whether this also supports crops which are nutritionally and morphologically less favourable to key aphid pests.

MATERIALS AND METHODS

Study Design

In 2014, eight pairs of conventionally managed winter wheat fields in each of the UK, the Netherlands, Sweden and nine pairs in both Germany and Poland were selected for this study. Within each field pair, one field had low and one high soil organic carbon (SOC) due to contrasting soil management history. We use soil organic carbon as a proxy for total soil organic matter (SOM) to standardise and compare the effects of SOM across study sites with varying soil types and management histories. Previous management varied between fields and field pairs, both within and between countries. Management differences between fields included organic fertiliser application, tillage practice, previous field use and crop rotation (see Table S1 for details of field management history). Differences in SOC were validated with soil core analysis. Mean SOC in UK sites was 1.48%

(SD \pm 0.57) for high sites and 1.05% (SD \pm 0.30) for low sites; Netherlands averaged 2.00% (SD \pm 0.23) in high sites and 1.39% (SD \pm 0.30) in low sites; in Sweden, high sites had 1.95% (SD \pm 0.049) SOC and low sites 1.89% (SD \pm 0.042); in Germany, high sites averaged 1.63% (SD \pm 1.03) and low sites 1.20% (SD \pm 0.49); and finally SOC content in Poland was 1.26% (SD \pm 0.49) for high sites and low sites had 0.84% SOC (SD \pm 0.24). Other factors such as local semi-natural habitat in a 1-km radius around the field, pH and soil texture were matched as far as possible within-field pairs (see Table S1 for soil pH and texture), and in most cases field sites were closer to their paired field than to fields in other pairs. In the UK, within-pair and between-pair mean separation was 2.02 km (SD \pm 1.7) and 4.98 km (SD \pm 3.8), respectively. In Sweden, within-pair separation was 0.43 km (SD \pm 0.34) and between pair was 12.68 km (SD \pm 8.46); in Germany, separation was 1.25 km (SD \pm 0.99) within pairs and 11.21 km (SD \pm 3.75) between pairs, whereas in Poland within- and between-pair separation was 4.45 km (SD \pm 1.8) and 14.76 km (SD \pm 5.08), respectively. Finally, due to high soil variability at the Netherlands sites, to ensure pairs had matching soil type and local landscape context, it was not always possible to pair fields geographically. All fields were located in a single study region with a mean field separation of 1.75 km (SD \pm 1.58) overall.

In each of the 84 fields, two experimental study plots measuring at least 14 \times 12 m were set up adjacent to the field boundary. One plot received mineral nitrogen fertiliser in accordance with regional standard practices, whereas the other received no fertiliser. Nitrogen fertiliser was applied by hand in the fertilised plots at the following dose rates: 90 kg N/ha in Poland (ammonium nitrate), 170 kg N/ha in the Netherlands (calcium ammonium nitrate) and Sweden (ammonium nitrate) and 190 kg N/ha in Germany (ammonium sulphate nitrate) and the UK (ammonium nitrate). Farmers applied fungicides and herbicides in line with standard practice, but no application of insecticides to the plots was carried out.

Wheat Growth and Yield

To estimate effects on wheat growth and yield of SOC and nitrogen fertiliser, four random subplots of 0.25 m² were harvested from each plot and then pooled, dried in a 70°C oven for 24 h and threshed to get estimated grain weight in tonnes per hectare per plot. To investigate treatment effects on wheat

growth metrics, at the time of harvest, a whole wheat plant was collected within each harvested subplot. These plants were cut at ground level and dried in a 70 °C oven for 24 h. They were weighed to establish total aboveground dry mass and then the ears were cut from the tillers and the weight of each was recorded. The summed weights per plant were then divided by the total number of tillers on each plant to establish an average 'tiller mass', 'ear mass' and 'aboveground biomass' per tiller per plot. The ratio of tiller mass to ear mass was then used to calculate 'harvest index', so investments by the plants in vegetative or reproductive tissue could be assessed.

Aphid Field Populations

To assess aphid populations across sites, study plots were visited three times during the season: between wheat tillering and stem elongation (BBCH 20–40), at booting and heading (BBCH 40–60) and at flowering and grain filling (BBCH 60–80). The abundance of *Metopolophium dirhodum*, *Rhopalosiphum padi* and *Sitobion avenae* within each plot was recorded by sampling 50–100 randomly selected tillers along transects located at least 10 m away and parallel to the field edge. To establish pest pressure for each species of aphid, aphid days per tiller were calculated. Aphid days represent the accumulated number of aphids per tiller per day (Ruppel 1983) and are calculated using the average number of aphids of each species observed on each tiller and the date on which aphid numbers were counted. The accumulated number of aphid days per tiller between the first and last count was used for analyses.

Aphid Cage Study

To investigate bottom-up effects of SOC, nitrogen fertiliser and crop morphology on aphid population growth in the absence of (top-down) control by natural enemies, a cage trial was implemented at the UK study sites. At the wheat booting stage, an *S. avenae* population was established in each study plot of the 16 fields by inoculating a 25 cm by 25 cm area of crop with 50–100 aphid nymphs. The aphid populations were covered with temporary fibre tents to avoid predation and left for 10 days to allow for successful establishment of aphids. For the cage study, wheat plants supporting the aphids were then covered with a plastic mesh cage measuring 30 cm width by 1.5 m height. A metal cylinder, 20 cm depth, was placed around the base of the cage and buried 10 cm into the ground to exclude ground active natural enemies. Addition-

ally, the cage was sprayed with glue to prevent areal predators reaching the aphid population. The experiment was initiated by counting the number of aphids on all tillers within the cage. After 5 days, the plots were revisited and the numbers of aphids on all tillers within the cage were again recorded to determine how aphid populations had changed in this time. The ratio of final to initial aphid numbers within each cage was used as a measure of population growth rate.

Statistical Analysis

To test the effects of SOC and nitrogen fertiliser application on wheat growth metrics (harvest index, tiller mass, ear mass and aboveground biomass), yield and aphid abundance in the field and how this varied between study regions, linear mixed effects models were used. SOC (high, low), fertiliser (yes, no), country (Germany, Poland, Sweden, Netherlands and UK) and their interactions were included in the models as main effects. Field nested within-field pair was included as a random effect. Harvest index, ear mass and aboveground biomass were log transformed prior to analysis to improve normality. Aphid days per tiller for all three species were inverse hyperbolic sine (IHS) transformed before analysis to improve normality and to account for zeroes in the data. In some countries, certain aphid species were recorded in very low numbers (< 5 individuals observed in total), and these countries were excluded from the analysis for that aphid species. Thus, data from Germany and Poland were not included in the analysis for *Metopolophium dirhodum*, as were UK and Polish data for *Rhopalosiphum padi* analysis. *Sitobion avenae* was found in sufficient abundance in all countries. Model selection was based on the lowest Akaike information criterion (AIC) score compared between models containing main effects and all possible interactive effects, and model fit was checked by visual observation of residuals.

To investigate the relationship between wheat growth metrics and aphid populations, linear mixed effects models were used, relating the abundance of aphid species expressed as IHS transformed aphid days to wheat tiller mass, ear mass, harvest index and aboveground biomass. Country was also included in the model as a main and interacting factor. Ear mass, harvest index and aboveground biomass were log transformed prior to analysis. The same nested random structure as in previous models was used.

Data from the UK cage trial were analysed using linear mixed effects models to investigate effects of

SOC and fertiliser treatment on aphid performance measured as ‘population growth rate’. The aphid population in one study plot was lost, and one was unexplainably high during the second count; therefore, both these data points were removed from the analysis. Linear mixed effects models were also used to investigate the relationship between crop growth metrics and population growth rate. Field nested within-field pair was included as a random factors, and lowest AIC score was used to select the most appropriate model which at least retained main effects. Analyses were carried out in R version 3.3.1, and linear mixed models were run using the ‘nlme’ package (R Core Development Team 2015).

RESULTS

Across all countries, grain yield per plot was significantly affected by SOC and nitrogen fertiliser application, but not by their interaction (Table 1). A significant interaction effect of nitrogen fertiliser and country was found. Yield was on average 10% greater in plots with high SOC compared to those with low SOC (8.1 vs. 7.3 t/Ha), whereas fertilised plots produced approximately 30% greater yield than unfertilised plots (9.3 vs. 6.1 t/Ha) (Figure 1). Nitrogen fertiliser application had a significant positive effect on tiller mass, ear mass and aboveground biomass, independent of SOC (Table 1). All wheat growth metrics were significantly affected by country, yet for harvest index, this effect depended on the application of nitrogen fertiliser.

Sitobion avenae aphid numbers varied among countries, but their abundance in aphid days per tiller was not affected by any experimental treatment (Table 2; Figure 1). By contrast, *M. dirhodum* was significantly affected by nitrogen fertiliser application (Table 2) with more than four times as many aphid days per tiller in fertilised compared to unfertilised plots (Figure 1). We found no effect of SOC, although country was a significant factor. No experimental treatment or country effects on *R. padi* aphid days per tiller were observed (Table 2; Figure 1).

Crop growth metrics correlated with aphid species differently (Figure 2). *Sitobion avenae* aphid days per tiller were negatively associated with ear mass ($t = -2.82$, $P = 0.0062$) and aboveground biomass ($t = -2.37$, $P = 0.020$). A significant interaction between country and ear mass ($F_{4-74} = 3.22$, $P = 0.017$), aboveground biomass ($F_{4-74} = 3.26$, $P = 0.016$) and tiller mass ($F_{4-74} = 4.52$, $P = 0.003$) was also seen with a prominent negative relationship with *S. avenae* numbers seen in

Sweden and Germany (Figure S1). *Metopolophium dirhodum* were positively associated with tiller mass ($t = 3.76$, $P = 0.0005$), ear mass ($t = 2.30$, $P = 0.026$) and aboveground biomass ($t = 3.55$, $P = 0.0009$) (Figure 2), and there was a significant tiller mass–country interaction ($F_{2-45} = 3.79$, $P = 0.03$). Significant interactions between country and harvest index ($F_{1-45} = 3.32$, $P = 0.045$) and country and aboveground biomass ($F_{1-45} = 4.83$, $P = 0.013$) on *M. dirhodum* aphid days per tiller were found with clear positive relationships seen in UK and Netherlands (Figure S2). *Rhopalosiphum padi* aphid days per tiller were higher on plants with greater tiller mass ($t = 2.18$, $P = 0.034$) (Figure 2).

There was a significant positive effect of SOC on tiller mass ($F_{1-7} = 9.47$, $P = 0.018$), ear mass ($F_{1-7} = 10.98$, $P = 0.013$) and aboveground biomass ($F_{1-7} = 11.16$, $P = 0.012$) in the UK cage trials (Figure 3). Only marginal effects of nitrogen fertiliser application on tiller mass ($F_{1-13} = 4.52$, $P = 0.053$) and ear mass ($F_{1-13} = 4.11$, $P = 0.064$) were found, whereas the effect on aboveground biomass was significant ($F_{1-13} = 5.40$, $P = 0.037$). There were no significant fertiliser–SOC interactions on tiller mass ($F_{1-12} = 1.28$, $P = 0.28$), ear mass ($F_{1-12} = 0.69$, $P = 0.42$) or aboveground biomass ($F_{1-12} = 0.64$, $P = 0.44$). The population growth rate of *S. avenae* in field cages was significantly greater in nitrogen fertilised compared to unfertilised plots ($F_{1-13} = 4.95$, $P = 0.045$), but no effect of SOC ($F_{1-7} = 0.87$, $P = 0.38$) or a fertiliser–SOC interaction was observed ($F_{1-12} = 0.071$, $P = 0.80$). *Sitobion avenae* population growth rate was also positively related to aboveground biomass ($t = 3.51$, $P = 0.038$) (Figure S4).

DISCUSSION

Using a large-scale, replicated field experiment, we quantify the potential to better utilise ecosystem services and identify a real-world opportunity to operationalise ecological intensification in arable cropping systems in Europe. Across our study regions, grain yield was significantly greater in fields with higher soil organic carbon (used as a proxy for soil organic matter), and replacement of conventional fertiliser application has the potential to reduce pest pressure from some aphid species. This study shows therefore that declining SOM in intensive arable systems compromises yield and limits the capacity to ecologically intensify crop production.

At levels found in our study regions, fields with greater organic matter content had a yield increase of approximately 10%, although no positive effects

Table 1. Effects of Soil Organic Carbon (SOC), Nitrogen Fertiliser, Country and Their Interactions on Wheat Growth and Yield for 84 Fields Across 5 European Countries

	Tiller mass			Ear mass (log)			Harvest index (log)			Aboveground (log)			biomass			Yield (T/ha)		
	d.f.	F value	P	d.f.	F value	P	d.f.	F value	P	d.f.	F value	P	d.f.	F value	P	d.f.	F value	P
Intercept	1,78	3041.899	< 0.0001	1,78	671.337	< 0.0001	1,74	446.219	< 0.0001	1,78	3565.531	< 0.0001	1,73	1461.643	< 0.0001	1,73	1461.643	< 0.0001
SOC	1,62	0.938	0.337	1,62	0.191	0.664	1,62	0.419	0.520	1,62	0.662	0.419	1,65	4.217	0.044	1,65	4.217	0.044
Nitrogen	1,78	24.631	< 0.0001	1,78	17.125	< 0.0001	1,74	0.512	0.476	1,78	22.435	< 0.0001	1,73	241.964	< 0.0001	1,73	241.964	< 0.0001
Country	4,62	19.509	< 0.0001	4,62	32.073	< 0.0001	4,62	24.565	< 0.0001	4,62	13.036	< 0.0001	4,65	2.819	0.032	4,65	2.819	0.032
SOC–nitrogen	1,69	3.650	0.060	1,69	3.148	0.080	1,69	1.610	0.209	1,69	3.308	0.073	1,73	2.770	0.100	1,73	2.770	0.100
SOC–country	4,58	0.710	0.584	4,58	1.353	0.261	4,58	0.654	0.627	4,58	1.223	0.311	4,65	0.811	0.523	4,65	0.811	0.523
Nitrogen–country	4,69	2.400	0.058	4,69	0.977	0.426	4,74	8.245	< 0.0001	4,69	0.844	0.502	4,73	6.826	< 0.0001	4,73	6.826	< 0.0001
SOC–nitrogen–country	4,69	1.515	0.208	4,69	0.491	0.742	4,69	0.570	0.686	4,69	0.842	0.503	4,73	0.333	0.855	4,73	0.333	0.855

Outputs from analysis using linear mixed effects models shown. Significant treatment effects ($P > 0.05$) in bold

on wheat harvest index were found. The mechanisms involved may include a number of physical, chemical and biological factors supported by soil organic matter (Reeves 1997) and that underpin key regulating and supporting ecosystem services (Adhikari and Hartemink 2016). Readily available nitrogen from synthetic sources also clearly makes an important contribution to yield by promoting tillering and increasing crop biomass, and modern varieties of cereal are bred to respond well to synthetic fertilisers (Dawson and others 2008). Application of nitrogen fertilisers resulted in an average yield increase of approximately 30% in this study. Accordingly, higher SOM could not offset fertiliser application completely, but soil management practices that promote SOM build-up such as reduced tillage, crop diversification, including legumes in the rotation and organic fertiliser addition (Drinkwater and others 1998; Edmeades 2003; Kremen and Miles 2012) could reduce the need for high application rates of synthetic fertiliser in the longer term through improved nitrogen availability and nitrogen use efficiency (Maeder and others 2002; Blesh and Drinkwater 2013). The risk of yield deficits following transition away from heavy use of conventional fertilisers may become acceptable if the wider ecosystem benefits of increasing SOM and reduced fertiliser application are considered, such as carbon sequestration (Lal 2004) and reduced environmental pollution (Zhu and Chen 2002). In this study, we use soil organic carbon (SOC) as a proxy for total soil organic matter (SOM) to standardise and compare the effects of SOM across study sites with varying soil types and management histories. Soil organic matter exists in many forms and is of variable quality (Marriott and Wander 2006; Schmidt and others 2011). Although SOC content is not necessarily a direct measure of SOM or of overall soil health, the beneficial effects of SOC demonstrated in this study reflect the overall benefits of management practices that increase the amount of carbon in the soil (eg. organic fertiliser, minimum tillage, diverse rotations) and influence quantity and quality of the soil organic matter.

A potential additional benefit of full or partial replacement of mineral fertiliser and increased SOM could be fewer pests in crops, thus reducing the reliance on plant protection products and supporting ecological intensification. Several ecological hypotheses have relevance when considering the response of herbivorous pests to bottom-up effects of SOM and fertiliser treatments. These include the ‘plant vigour hypothesis’ (Price 1991), the ‘plant stress hypothesis’ (White 1969, 2009), the ‘mineral

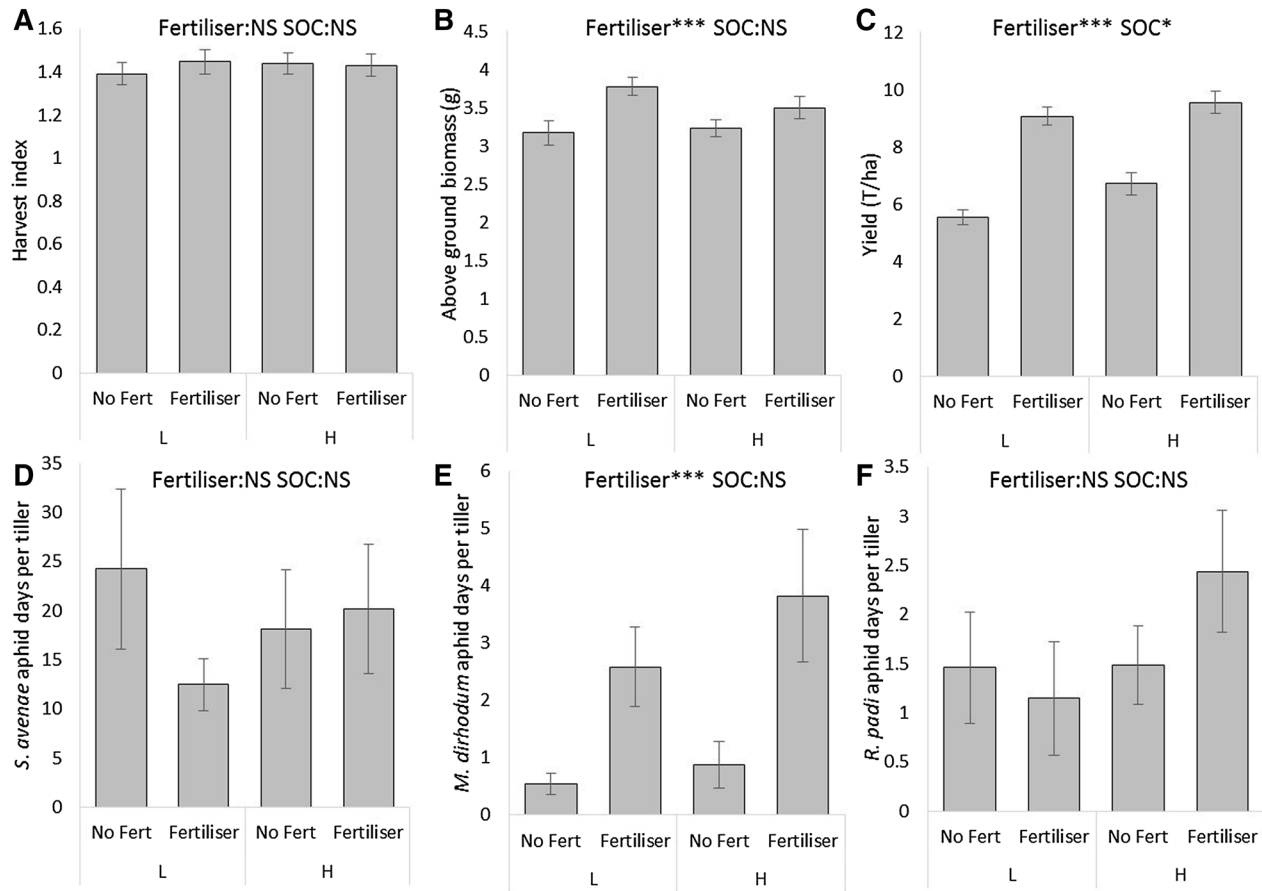


Figure 1. Effects of soil organic carbon (SOC) content (L = low, H = high) and nitrogen fertiliser (No Fert = no application, Fertiliser = applied at local rates) on wheat growth **A** harvest index, **B** aboveground biomass (g), **C** yield (T/ha) and aphid populations in aphid days per tiller of **D** *Sitobion avenae*, **E** *Metopolophium dirhodum* and **F** *Rhopalosiphum padi* from wheat fields across Europe. Mean ± SE. Significant effects of SOC and fertiliser shown following analysis using linear mixed effect models ($P = * < 0.05$, $** < 0.01$, $*** < 0.001$).

Table 2. Effects of Soil Organic Carbon (SOC), Nitrogen Fertiliser, Country and Their Interactions on the Abundance of Three Aphid Species on Wheat Measured in Aphid Days per Tiller from 84 Fields Across 5 European Countries

	<i>Sitobion avenae</i>			<i>Metopolophium dirhodum</i>			<i>Rhopalosiphum padi</i>		
	d.f.	F value	P	d.f.	F value	P	d.f.	F value	P
Intercept	1,78	563.920	< 0.0001	1,45	126.380	< 0.0001	1,48	53.400	< 0.0001
SOC	1,62	0.037	0.848	1,37	1.145	0.292	1,38	2.678	0.110
Nitrogen	1,78	0.068	0.796	1,45	60.951	< 0.0001	1,48	0.400	0.530
County	4,62	57.574	< 0.0001	2,37	41.399	< 0.0001	2,38	2.898	0.067
SOC–nitrogen	1,69	3.425	0.069	1,42	0.796	0.377	1,43	1.687	0.201
SOC–country	4,58	0.316	0.866	2,35	0.374	0.691	2,36	0.151	0.860
Nitrogen–country	4,69	1.373	0.252	2,45	13.497	< 0.0001	2,43	0.333	0.719
SOC–nitrogen–country	4,69	0.760	0.555	2,42	1.070	0.352	2,43	0.310	0.735

Outputs from analysis using linear mixed effects models shown. Significant treatment effects ($P > 0.05$) in bold.

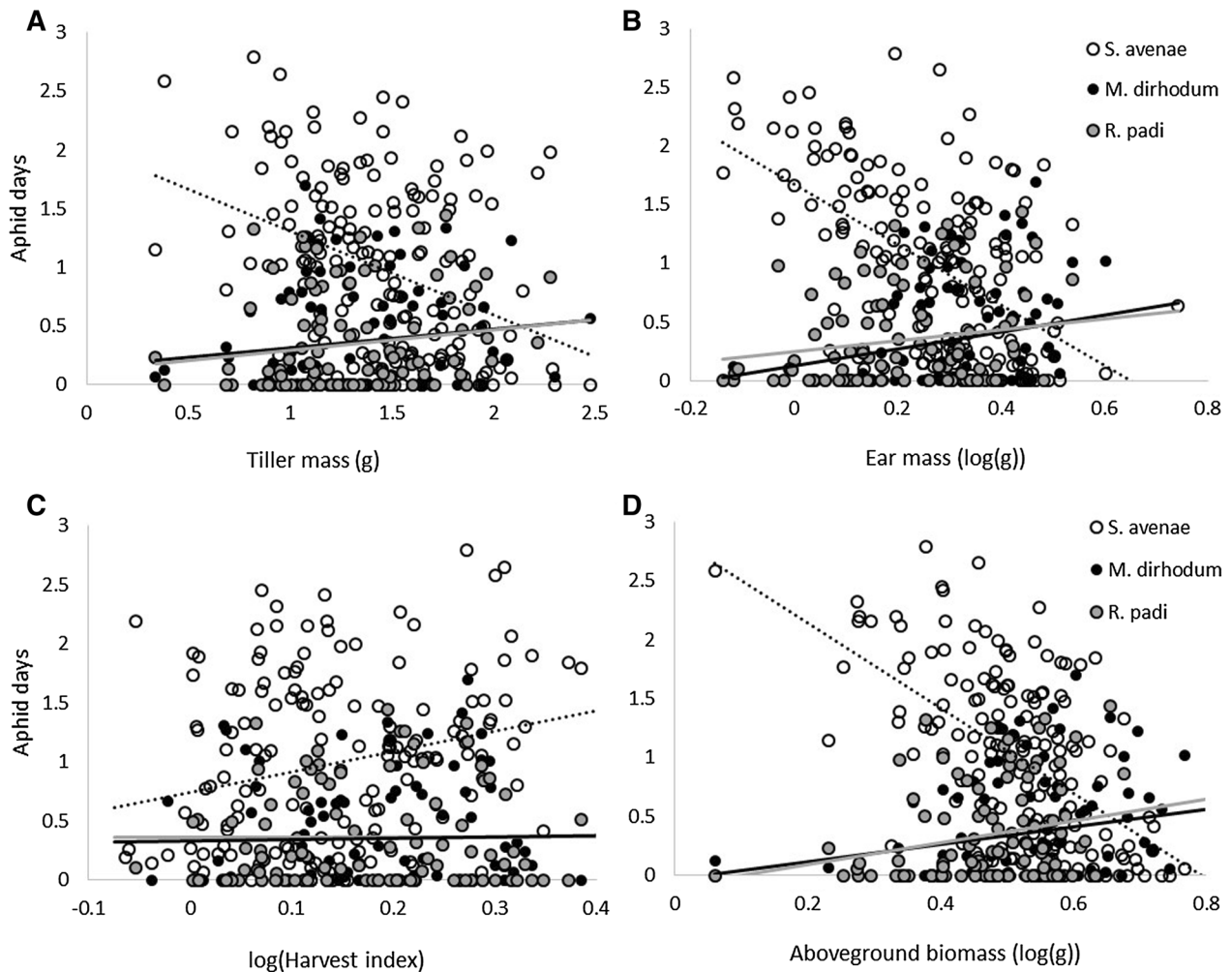


Figure 2. Relationship between wheat growth metrics **A** tiller mass (g), **B** ear mass (log(g)), **C** log harvest index and **D** aboveground biomass (log(g)) and aphid populations in aphid days per tiller (inverse hyperbolic sine transformed) of *Sitobion avenae*, *Metopolophium dirhodum* and *Rhopalosiphum padi* from wheat fields across Europe.

balance hypothesis' (Phelan and others 1996) and the 'N-damage hypothesis' (Matson and others 1997). The plant vigour and plant stress hypotheses are somewhat contradictory; one proposes that herbivores will perform better on vigorous, fast growing hosts, whereas the other states that stressed plants are nutritionally more favourable to herbivores, although the response of pests depends on their feeding habit (White 2009). The N-damage hypothesis suggests a positive relationship between host nitrogen content and damage by herbivores, whereas the mineral balance hypothesis states that positive soil functioning will be conveyed to host plants making them better able to resist pests.

In the present study, field populations of *Metopolophium dirhodum* were considerably greater in fertilised plots, and on tillers with greater biomass. Plants well supplied with nitrogen invest in vege-

tative growth and can therefore support greater numbers of pest species such as the leaf-feeding aphid *M. dirhodum* (Watt 1979). Similar positive effects of plant morphology on *M. dirhodum* have been observed in other studies (Honěk and Martinková 2002; Honek and others 2006; Garratt and others 2010b). The leaf-feeding aphid *R. padi* (Leather and Dixon 1981), although not directly affected by experimental treatments, was also positively associated with plants of greater tiller mass in this study. The positive relationship between crop biomass and both these aphid species is consistent with the plant vigour hypothesis (Price 1991), with aphids performing better on fast growing, larger wheat plants. Positive effects of nitrogen application on insect abundance and performance are a consistent trend across both

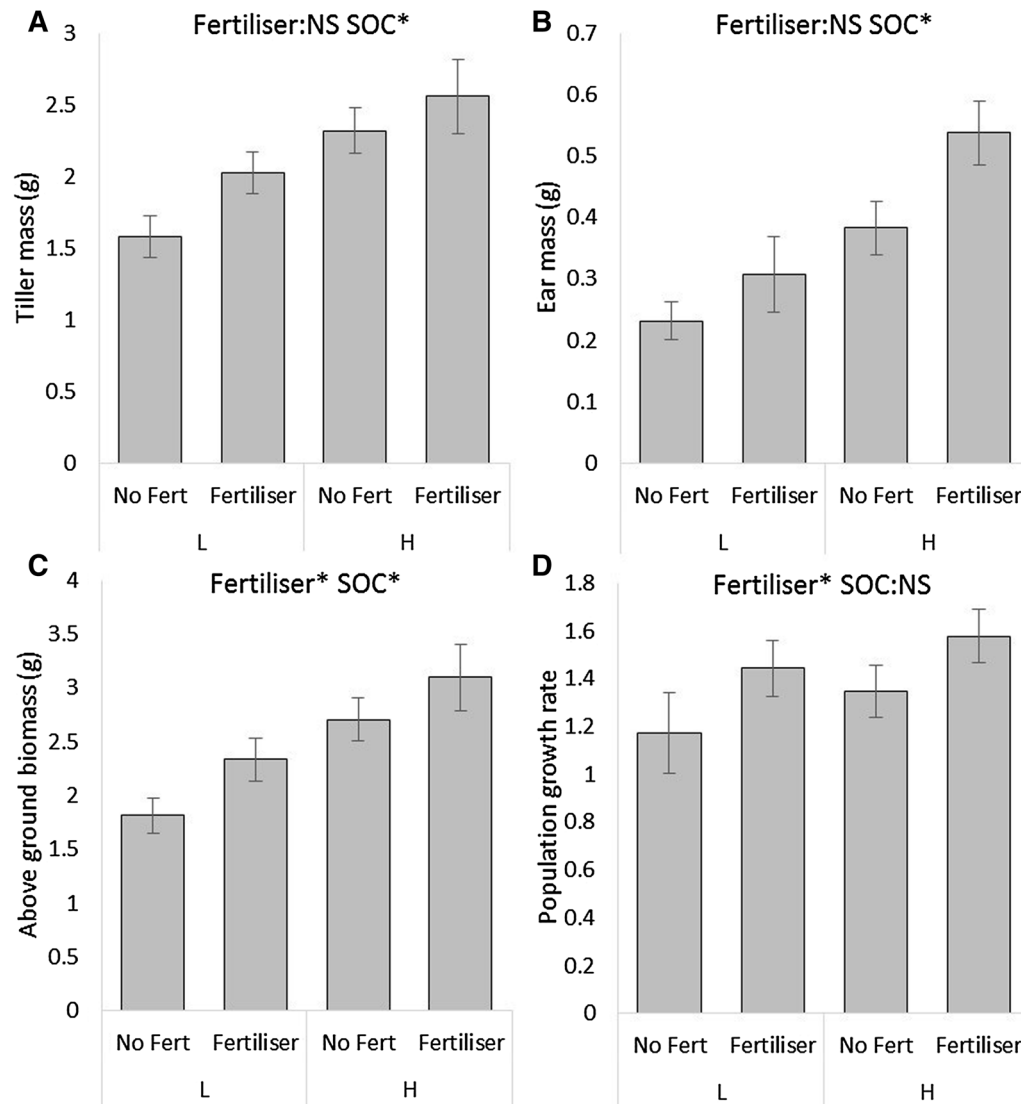


Figure 3. Effects of soil organic carbon (SOC) content (L = low, H = high) and nitrogen fertiliser (No Fert = no application, Fertiliser = applied at local rates) on wheat growth **A** tiller mass, **B** ear mass, **C** aboveground biomass and **D** *Sitobion avenae* populations growth in exclusion cages in UK wheat fields. Mean \pm SE. Significant effects of SOC and fertiliser shown following analysis using linear mixed effect models ($P = * < 0.05$, $** < 0.01$, $*** < 0.001$).

agricultural and natural ecosystems, particularly for sucking pests (Butler and others 2012).

Sitobion avenae population growth rates in the field cage trial responded positively to nitrogen fertiliser application, and there was a significant positive correlation with aboveground biomass. This indicates that bottom-up effects of nitrogen fertiliser improve aphid population growth of this species as well, probably due to improved host nutritional quality or morphology (Aqueel and Leather 2011). However, in contrast to *M. dirhodum*, *S. avenae* abundance in the field was not increased by fertiliser application and it was not influenced by SOM. Populations were also nega-

tively associated with wheat ear mass and above ground biomass. This demonstrates that indirect effects of nitrogen fertiliser and SOM, or other independent factors, are driving their populations in the field. The capacity to reduce populations of this species through reduced fertiliser application therefore may be limited. For example, *S. avenae* abundance might depend on landscape factors affecting migration, colonisation or pest control by its natural enemies (Martin and others 2015; Bøsem Baillod and others 2017) independent of soil management. Alternatively, nitrogen fertiliser application and/or SOM may be affecting natural enemies of *S. avenae* directly by influencing natural

enemy fitness or by providing alternative food sources, and this is fed back to altered levels of pest control (Scheu 2001; Birkhofer and others 2008; Garratt and others 2010a). Lastly, high *S. avenae* populations may affect crop growth and result in reduced aboveground biomass, evidenced by negative associations with crop biomass in countries with greater aphid densities, namely Germany and Sweden (Figure S1). More research is needed to fully understand these complex interacting effects.

Given the benefits of SOM for yield demonstrated by this and numerous other studies, and the consequences of nitrogen fertiliser application on increased pest performance, incorporating management practices that maintain or increase organic matter in agricultural soils for partial replacement of nitrogen fertilisers provides an opportunity for the ecological intensification of arable systems. Increasing in-field crop diversity (Kremen and Miles 2012; McDaniel and others 2014), introducing legumes into a rotation (Drinkwater and others 1998), reduced tillage practices (Mangalassery and others 2015) or application of organic fertilisers (Edmeades 2003; Plaza and others 2016) can all increase SOM in agro-ecosystems and reduce reliance on nitrogen fertilisers.

To promote ecological intensification of agriculture, both the private (e.g. yield, pest control) and wider public (e.g. climate change mitigation, reduced environmental pollution) ecosystem goods and services need to be considered together. Policy should be enacted (e.g. through agri-environment schemes) to buffer possible short-term yield penalties and support farmers to ecologically intensify arable production. Sustainable production of cereal crops in Europe will ultimately depend on an integrated approach that considers potential replacement of high inputs of conventional fertilisers and insecticides with management practices that increase SOM and promote better natural pest control. It may not be possible to replace conventional fertilisers entirely and still achieve the same yield; however, if the environmental benefits of reduced fertiliser application and increased SOM are considered, then a yield cost may be acceptable.

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