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Soil Organic Matter as Catalyst of Crop Resource Capture

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The positive effect of soil organic matter (SOM) on crop yield has historically been attributed to the ability of SOM to supply crops with nitrogen and water. Whether management-induced increases in SOM meaningfully supplement water supply has received recent scrutiny, introducing uncertainty to the mechanisms by which SOM benefits crops. Here, we posit that to benefit crops SOM does not need to increase the supply of a growth-limiting resource; it only needs to facilitate root access to extant resource stocks. We highlight evidence for the ability of SOM to alleviate negative impacts of inadequate aeration (mainly waterlogging) and compaction on roots. Waterlogging, even if transient, can permanently downregulate root biosynthesis and call for expensive growth of new roots. Management practices that promote SOM reduce waterlogging by accelerating water infiltration and may promote aeration in non-saturated soils. Compaction as a restriction to root development manifests in drying soils, when mechanical impedance (MI) inflates photosynthate required to extend root tips, leading to short, thick, and shallow roots. SOM reduces MI in dry soils and is associated with root channels to subsoil, granting crops access to deep soil water. Both waterlogging and compaction necessitate additional belowground investment per unit resource uptake. In this framework, crop response to SOM depends on interactions of crop susceptibility to inadequate aeration or compaction, soil moisture, and "baseline" soil aeration and compaction status. By exploring the proposition that SOM catalyzes resource uptake by permitting root development, future research may constrain crop yield improvements expected from SOM management.

Keywords: aeration, available water capacity, compaction, crop yield, mechanical impedance, soil health and quality, soil organic matter, waterlogging

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INTRODUCTION

Despite comprising a small proportion of the mass of agricultural soils, soil organic matter (SOM) is associated with improved soil structure (Feller and Beare, 1997; Six et al., 2000; Dexter et al., 2008; King et al., 2019). Multiple features of agricultural systems limit the extent by which management can alter SOM levels, but managing for even a modicum of increased SOM offers societal benefits, including climate change mitigation from the storage of carbon (C; Paustian et al., 2016; Minasny et al., 2017), a component of SOM, and reduced erosion (Barthès and Roose, 2002). Another, potential benefit of SOM is increasing crop yield (Pan et al., 2009; Oldfield et al., 2018), however, we have limited ability to explain inconsistent effects of management-induced increases in SOM on crops (Xin et al., 2016; Bradford et al., 2019; Wade et al., 2020) or to constrain potential crop benefits from SOM in future climates, as crop stressors shift (IPCC, 2019). Progress on these fronts relies on a sound understanding of mechanisms through which SOM benefits crops in the first place.

Historically, improved crop yield from SOM has primarily been attributed to SOM's role in resource supply, either of water or nitrogen (Gregorich et al., 1994; Arshad and Martin, 2002; Lal, 2020). A large effect of SOM on available water capacity (AWC) was established without consideration of limits of management-induced SOM (Hudson, 1994). A recent synthesis, however, concluded that management-induced increases in SOM (10 g C/kg soil) effected on average only 1.16 mm additional AWC in the top 10 cm of soil (Minasny and McBratney, 2018). This is a limited contribution to crop transpiration, which can exceed 450 mm (Kimball et al., 2019, maize). If a 1.16 mm increase in SOM-derived AWC is multiplied by rain events during crop maturation, signifying the number of times AWC is "used," and including 10–20 cm soil, the augmentation of AWC by SOM is larger, but an effect on crop performance is likely context-dependent. While SOM is linked to AWC and management increases AWC in some situations, crop water supply does not appear well-justified as a universal mechanism linking management-induced SOM increases to crop yield.

Larger SOM pools are linked to higher production rates of plant-available nitrogen (N) via net N mineralization (Schimel, 1986; Booth et al., 2005), leading to the view that SOM benefits crops by increasing N supply. However, to determine that N supply from SOM limits crop growth, rates of plant N uptake should approach rates of N mineralization, indicating a potential for crop N demand that outpaces soil N supply. Results of this comparison depend on method, with net N mineralization deceeding (Brye et al., 2003; Loecke et al., 2012) but gross N mineralization exceeding (Osterholz et al., 2016) crop N demand. If gross N mineralization is indeed a better indicator of plant-available N than net N mineralization (Schimel and Bennett, 2004), or an underestimate given crop uptake of amino acids (Hill et al., 2011), then increasing SOM would simply be increasing an already sufficient N supply.

Here, we posit that SOM benefits crops not necessarily by increasing resource supply but by catalyzing crop resource capture (**Figure 1**). Roots, the locus of nutrient and water uptake, rely on contact with soil for nutrient (Wang et al., 2006), and water uptake (Javot and Maurel, 2002). Vigorous root development therefore multiplies the surface area of root-soil contact through which resource uptake occurs. We highlight below the consequences of inadequate aeration and compaction on roots and the ability of SOM-enhancing management practices to alleviate these stressors. While we acknowledge that relationships between SOM and soil structure are known (Karlen et al., 2001; Bünemann et al., 2018), we argue that their connections to related crop stressors—poor aeration and compaction—have received inadequate attention as mechanisms that link SOM to crops. We also acknowledge that compaction and inadequate aeration are often co-located, and we separate them to discuss how they manifest differently in the soil environment and as root stressors.

We refer to differences in SOM induced by agricultural practices, such as cover crops (Poeplau and Don, 2015), perennial forages (King and Blesh, 2018), manure application (Maillard and Angers, 2014), straw retention (Liu et al., 2014), or reduced tillage (in surface soil, Luo et al., 2010), except where noted. Although some of the mechanisms discussed may apply to naturally occurring variability in SOM, we defer their discussion for brevity.

AERATION

Inadequate Aeration in Waterlogged and Non-saturated Soils

As a substrate for respiration, O_2 and its transport potentially affect all functions of crop roots (Grable, 1966). To study the effects of O_2 deficiency in the field, researchers commonly impose an extreme constriction of aeration with waterlogging, the saturation of soil pores with water (Hodgson and Chan, 1982; Bange et al., 2004). Our consideration of inadequate aeration focuses accordingly on waterlogging, and we do not review impacts of inadequate aeration in non-saturated soils on crops, as these remain largely unexplored.

Waterlogging, Even if Transient, Can Indelibly Damage Roots

Waterlogging damages diverse crops worldwide (Velde and Van Der Tubiello, 2012; Shaw et al., 2013; Zhang et al., 2015; Li et al., 2019), and increases in waterlogging due to climate change are forecasted to exacerbate these damages (Rosenzweig et al., 2002). Waterlogging reduces soil aeration due to a 10^4 fold slower rate of O_2 diffusion through water than through air (Grable, 1966). Within hours, soil O_2 can be depleted as root or soil organisms' respiration demands exceed atmospheric O_2 supply, with rate and extent of O_2 depletion depending on depth (Malik et al., 2001) and temperature (Trought and Drew, 1982). Over slightly longer time frames, waterlogged soils also accumulate byproducts of root or microbial metabolism, e.g., CO_2, Fe^{2+}, and Mn^{2+}, potential plant toxins (Shabala, 2011). Crop responses to waterlogging depend on crop species and cultivar (Huang, 1997; Boru, 2003; Ploschuk et al., 2018), as well as timing (Rhine et al., 2010; de San Celedonio et al., 2014; Ren et al., 2014) and duration (Malik et al., 2002; Rhine et al., 2010; Kuai et al., 2014; Ren et al., 2014; Arduini et al., 2019) of waterlogging, but a well-supported view holds that crop yield reductions from waterlogging are largely attributable to impaired function and inadequate recovery of roots (Malik et al., 2002; Herzog et al., 2016; Arduini et al., 2019).

In crops that are susceptible to waterlogging, stress response can be considered both during and after release from waterlogging. During waterlogging, O_2 deficiency induces an energy crisis in the root due to inefficient production of ATP (Gibbs and Greenway, 2003), which curtails energy-dependent nutrient uptake (Trought and Drew, 1980; Morard et al., 2000; Colmer and Greenway, 2011) and root growth (Palta et al., 2010; Arduini et al., 2019). After release from waterlogging,

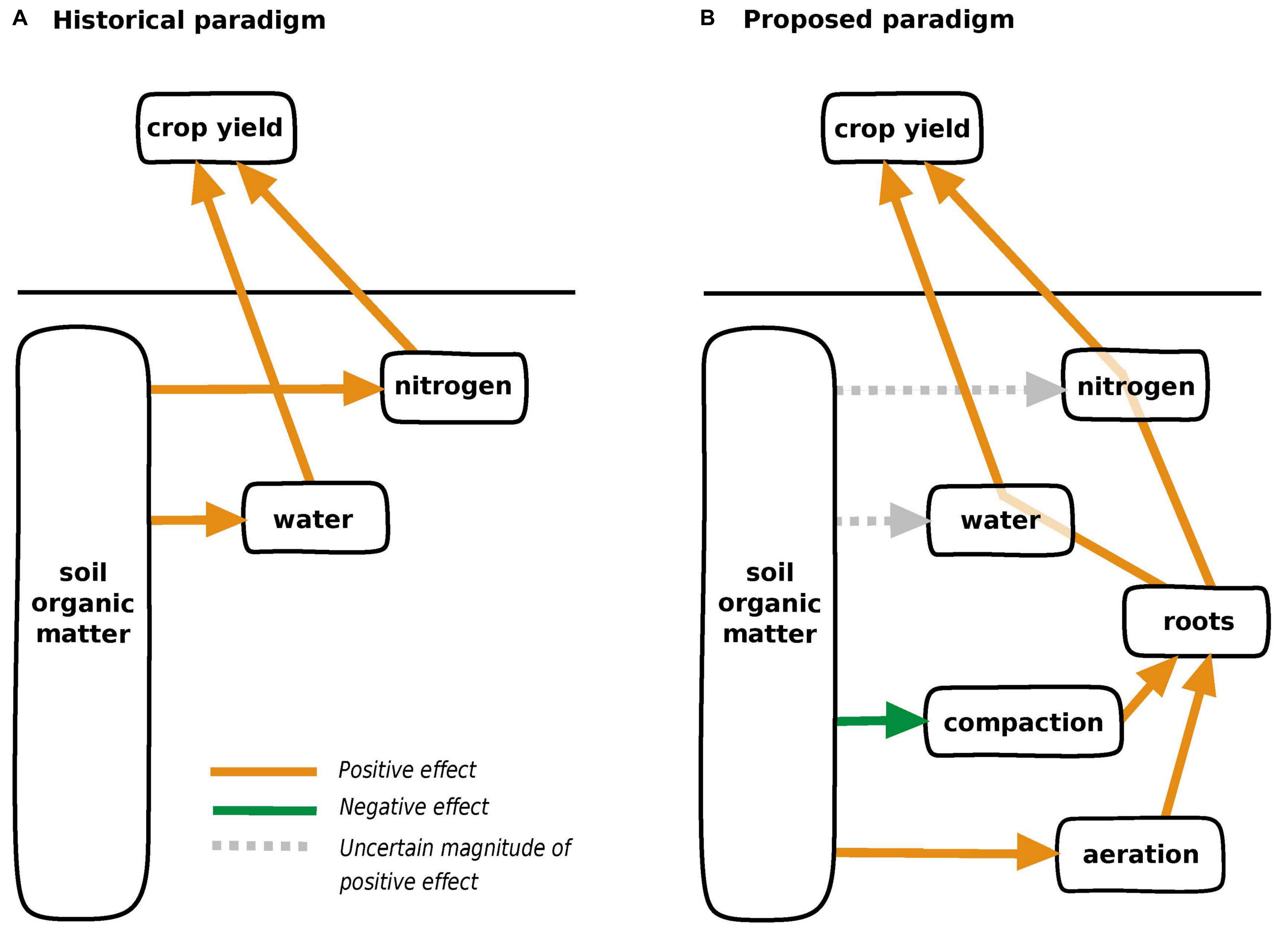

FIGURE 1 | Conceptual models representing **(A)** historically acknowledged and **(B)** newly proposed mechanisms linking management-induced increases in soil organic matter with crop yield. We recognize that the effect of SOM in mediating soil structure has been known for decades, but we argue that exploring the response of crops to related stressors (inadequate aeration and compaction) has potential to explain effects of SOM on crop yield.

root growth of certain root forms, i.e., seminal roots, can be permanently inhibited (Malik et al., 2002; Palta et al., 2010; Colmer and Greenway, 2011), attributable to cell death in apical meristems (Trought and Drew, 1980; Malik et al., 2002), beyond the reach of plant-transported O_2 (Colmer and Greenway, 2011). Crops must then rely on energetically-expensive production of new roots, i.e., adventitious roots (Palta et al., 2010; Steffens and Rasmussen, 2016), and/or increase nutrient uptake per unit root (Arduini et al., 2019). These adaptations do not necessarily allow crops to escape a waterlogging yield penalty, as reductions in root biomass (Grassini et al., 2007; de San Celedonio et al., 2017; Ploschuk et al., 2018) or root length density (Hayashi et al., 2013) are often linked to reductions in shoot biomass or yield.

Uncertainty remains about the threshold duration at which waterlogging damages crops. In some crops and growth stages, waterlogging as short as 3 days reduced yield (Malik et al., 2002; Ren et al., 2014), but the shortest waterlogging we found in field studies was 2 days (Rhine et al., 2010). Due to the risk of crop damage from even transient waterlogging, there is interest in management practices that reduce waterlogging risk (Manik et al., 2019) and improve root aeration across the soil water spectrum (Rabot et al., 2018).

Soil Organic Matter: Means to Improve Root Aeration

Reducing Duration of Waterlogging

Management practices that promote SOM reduce risk and duration of waterlogging by increasing rate of water infiltration (Boyle et al., 1989; Adekalu et al., 2007; Abid and Lal, 2009; Blanco-Canqui et al., 2011), which increases the time soil can receive rain before ponding occurs (McGarry et al., 2000) and reduces time required to drain from saturation to field capacity (Wuest et al., 2005). Among the many measurable soil water variables, infiltration is the most commonly assessed, and we note the need to better establish relationships between infiltration, time to ponding, and drainage. It is also important to note, as reviewed by Blanco-Canqui and Ruis (2018) for no-till, that management practices that promote SOM can have a neutral effect on water infiltration in some cases, despite positive effects in majority of cases.

Accelerated infiltration associated with SOM is attributable to several soil features. The redistribution of soil mass to larger aggregate size classes associated with SOM (King et al., 2019) helps to explain an increase in total (Pikul and Zuzel, 1994; Yang et al., 2011; Blanco-Canqui and Benjamin, 2013) or macroporosity (>0.3–0.4 mm, Deurer et al., 2009; Yagüe et al., 2016), although this effect is not detectable in all cases (Ruiz-Colmenero et al., 2013). SOM also stabilizes aggregates (Chenu et al., 2000; Annabi et al., 2011), minimizing their dissolution into smaller, and pore-clogging size fractions that seal the soil surface against water infiltration (Bissonnais and Arrouays, 1997; Lado et al., 2004). The most dramatic effects of SOM on infiltration can likely be traced to earthworms and/or termites and their creation of wide, continuous, vertically-oriented pores through which water flows preferentially (McGarry et al., 2000; Guo and Lin, 2018). More abundant – or more active (Pérès et al., 2010) – soil fauna may be due in part to reduced disturbance associated with some SOM-promoting practices, e.g., no-till. However, close relationships between SOM and earthworm abundance without the confounding effect of disturbance (Fonte et al., 2009; Guo et al., 2016) also indicate a role for SOM as faunal substrate supply.

Few studies have attempted to link SOM-induced reductions in waterlogging with crop yield. Gómez-paccard et al. (2015), however, find crop yields increased from reduced surface soil waterlogging associated with no-till. The ability of SOM-mediated reductions in waterlogging to benefit crops are most likely when (1) crop is sensitive to waterlogging and (2) rainfall intensity can be mediated by SOM on a timescale relevant to waterlogging stress (neither drizzle nor deluge); and (3) soil is otherwise poorly-drained (Rhine et al., 2010).

Promoting Aeration in Non-saturated Soils

If crops experience inadequate aeration in non-saturated soils, it is reasonable to expect that SOM would improve gas diffusivity given its effects on related parameters of soil structure (Neira et al., 2015, and below). Few studies investigate the isolated effect of SOM on gas diffusivity, however, Colombi et al. (2019) find a positive relationship between SOM and gas diffusivity at field capacity across a soil texture gradient. Future work should examine net effects of SOM on O_2 diffusivity and consumption in soils.

COMPACTION

Soil Compaction Constrains Root Development

Soil compaction reduces crop yields (Coelho et al., 2000; Ishaq et al., 2001a; Bayhan et al., 2002; Czyz, 2004; Whalley et al., 2008) and is quantified via either bulk density or mechanical impedance (MI; Ehlers et al., 1987; Bengough et al., 2011). MI estimates the force encountered by the elongation of a living root, and is consequential for crops because greater MI inflates the photosynthate required for root elongation (Herrmann and Colombi, 2019). Although MI measurements ignore biopores used preferentially by roots (Stirzaker et al., 1996; White and Kirkegaard, 2010), MI is more descriptive than bulk density because it is sensitive to soil water. Drying soils present increasing MI (Vaz et al., 2011), and to isolate effects of water stress from compaction stress per se on crop development, researchers use experimental compaction.

Compaction studies indicate that reduced crop yield from compaction is due in large part to constraints on root development (Ishaq et al., 2001b; Czyz, 2004; Colombi and Keller, 2019). A root restricted by soil compaction is generally thicker than a root in non-compacted soil (Nadian et al., 1997), likely due to greater axial force needed to overcome compaction (Bengough, 2012). Reductions in total number of roots, rate of root elongation, total root length, or root biomass are also reported (Panayiotopoulos et al., 1994; Chan et al., 2006; Lipiec et al., 2012). Root length is generally more reduced than root dry mass (Panayiotopoulos et al., 1994), indicating the accumulation of belowground photosynthate without commensurate expansion of soil-contacting surface area available for nutrient and water uptake. Compaction is sometimes characterized by a hardpan around 20 cm depth, which leads to restricted root access to subsoil and concentrated root development in the topsoil (Czyz, 2004). This pattern of root development prevents crop access of deep soil water most implicated in crop drought resistance (Uga et al., 2013; Lynch, 2018).

A single threshold MI for crop sensitivity is unlikely to serve universally, and not only because cultivars (Houlbrooke et al., 1997) and crops (Rosolem et al., 2002) differ in MI tolerance. Threshold MI values also likely depend on definition by energy required to extend roots (Herrmann and Colombi, 2019) or by crop yield penalty. The MI required to reduce root growth efficiency is likely less than required to affect yields, and yield penalty due to restricted roots can be counteracted somewhat by fertilization (Robertson et al., 2009). Whatever the threshold, the detrimental effects of compaction on crops has generated attention toward means to reduce it.

Soil Organic Matter Reduces Compaction and Is Associated With Root Channels

Reduced Compaction: More Water Transpired Before Mechanical Impedance Limits Growth

Although SOM is often promoted for its ability to alleviate soil compaction and associated increases in MI (Hamza and Anderson, 2005), the generation of data confirming a negative SOM-MI relationship has been hampered by the convention of measuring MI in soils near field capacity (Duiker, 2002). Even in large datasets, no relationship between SOM and MI in soil near field capacity is found (Fine et al., 2017), likely because very wet soils (∼1–10 kPa) offer minimal MI regardless of SOM. It is as MI increases in drying soils (Vaz et al., 2011; Filho et al., 2014) that an effect of SOM becomes apparent (Stock and Downes, 2008; Gao et al., 2012).

We highlight two studies showing the effect of SOM in reducing MI as soils dry. Stock and Downes (2008) and

Gao et al. (2012) investigated soils differing only in SOM concentrations. With few exceptions, MI increased as soils approached permanent wilting point, but the increase in MI was not as much in higher SOM soils. In other words, SOM allows soil to become drier before reaching a potentially root-constraining MI. For instance, Stock and Downes (2008) find an MI of 1.5 MPa is reached in the 1% OM soil at $\sim$-100 kPa, whereas the 3% OM soil reaches the same MI at about $\sim$-200 kPa. For these soils, the difference in volumetric water content between -100 and -200 kPa is $\sim$0.02 m^{-3} H_2O m^{-3} soil, or $\sim$5 mm of water when considered over the top 25 cm. While Stock and Downes (2008) added organic amendments to glacial till to create fixed SOM percentages, their results resemble those of Gao et al. (2012), who compared fallow to grassland soils. The extent to which management-induced SOM benefits crops via reductions in compaction likely vary with context, particularly those relevant to MI thresholds (see section "Soil compaction constrains root development").

Root Channels to Subsoil Water

Although not connected to the physical or biological properties of SOM, management practices that promote SOM may also alleviate the effects of compaction by facilitating crop root access to the subsoil. Deep-rooted cover crops or perennial crops create root channels to subsoil (McCallum et al., 2004), which are used by subsequent cash crops (Rasse and Smucker, 1998; Williams and Weil, 2004). Crops are most likely to benefit from these root channels if subsoil is compacted and if crops experience sufficient water stress for subsoil water stores to be relevant.

DISCUSSION AND OUTLOOK

In the historical conceptual model linking crop performance to SOM, SOM benefits crops primarily by supplying nitrogen and water. Here we propose SOM as a mediator of resource uptake via root growth. We note caveats to the proposed framework. The extent to which SOM affects nutrient and water supply still merits research, and not all mechanisms discussed are contingent on increased SOM. We focus on MI to characterize compaction, but SOM may alter soil structure in ways relevant to root growth that are not captured by MI. As a simple diagram, **Figure 1** does not depict that yield penalty in low SOM soils may be due to cost of constructing new or thicker roots. However, considering SOM as catalyzing resource uptake via root development can help explain recent reports of SOM effects on crops. Wade et al. (2020) report maize yield increases from management-induced SOM across a range of N fertilizer levels, consistent with the concept that root N uptake—as well as soil N supply—can limit crop yield. Recognizing the importance of aeration for roots may also explain a parabolic crop response to a SOM gradient in a pot study (Oldfield et al., 2020), in which synthesized mixtures of minerals and organic horizons higher in SOM may have supported higher O_2 consumption by microbes without improved gas diffusivity expected in natural high-SOM soils (Colombi et al., 2019).

We propose the exploration of SOM as a catalyst for resource capture focuses on:

- *Characterizing the context-mediated effect of SOM on aeration and compaction* by describing the effect of SOM gradients on (a) aeration and risk and duration of waterlogging and (b) MI across a range of soil moisture contents.
- *Investigating crop response to SOM as a function of aeration and compaction* by identifying the thresholds of hypoxia affecting roots and yields. To relate SOM-mediated MI to root development, describing soil moisture status during crop maturation will be crucial.
- *Simulating future crop response to SOM*; currently, Basche et al. (2016) and Jarecki et al. (2018) are two of few examples to model the potential for management-induced SOM to stabilize crop yields under future climates.

We hope the lens proposed will help illuminate the effect of SOM on crops.

AUTHOR CONTRIBUTIONS

AK conceptualized and drafted the manuscript. GA, AG, and CW-R provided input to arrive at the final version.

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.