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Short Communication

Soil Nutrient Dependency of Biochemical Pathways for Synthesis of Plant Compounds

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Abstract

Micronutrient deficiency has been linked to various human diseases. Crops grown in mineral-depleted soils may have reduced food quality as measured by nutrient density because of any deficient minerals and a potential impaired ability to synthesize compounds essential to human health, including vitamins. Until recently, micronutrient density was not clearly understood and may have silently crept through the food chain, exacerbating various modern human diseases. We believe investigating the critical roles of soil micronutrients, especially magnesium (Mg) and zinc (Zn) in vitamin synthesis and function is urgently needed.

Keywords: Biochemical pathways, Magnesium, Micronutrients, Soil nutrient status, Zinc

Introduction

There is an increasing expectation that soil quality affects human health not just through food security (McGuire, 2015), but also through food quality (Bongaarts, 2021). Nutrient density is one measure of food quality, calculated as quantities of vitamins and minerals per kilocalorie of energy (Drewnowski and Fulgoni, 2014). However, it is challenging to connect soil characteristics, food quality, and human health: all are complex topics with multiple dimensions.

Bioinformatics databases have been used to link human diseases to human genes, genes to enzymes, and enzymes to vitamin and mineral cofactors (Scott-Boyer *et al.*, 2016; Ng *et al.*, 2015). These linkages suggest that dietary deficiencies of Mg or Zn could contribute to human diseases, including obesity, mood disorders, bronchial ailments, chronic obstructive airway diseases, and diabetes mellitus (see also Brinkman *et al.*, 2010; Ribaldone *et al.*, 2018; Godswill *et al.*, 2020; Pena *et al.*, 2020). Furthermore, obesity is linked to vitamins B2, B3, and C, and diabetes is linked to B1, B2, and B6 (Scott-Boyer *et al.*, 2016). Consequently, if soil deficiencies of Mg or Zn reduced the synthesis of vitamins B1, 2, 3, 6, or C in crops, then soil deficiency of either mineral would affect crop consumers directly, as a mineral deficiency, and indirectly through vitamin deficiencies. We examined the same databases that link human diseases to nutrients to look for connections between human nutrients and plant nutrients, specifically, divalent cation cofactors required by enzymes in vitamin synthesis pathways. We explore riboflavin (B2) synthesis as an illustrative case.

Soil is the ultimate source of most minerals for most terrestrial plants, with mineral extraction often being facilitated by a symbiotic microbiome of soil fungi and bacteria in healthy soils (Smith and Read, 2008). One measure of farm soil quality is its ability to provide essential elements for plants and support the synthesis of essential compounds for plants and people - vitamins, essential amino acids, and essential fatty acids. Farmers often add nitrogen, phosphate, and potassium fertilizers for crop production (Mandal *et al.*, 2009). Although minor and trace

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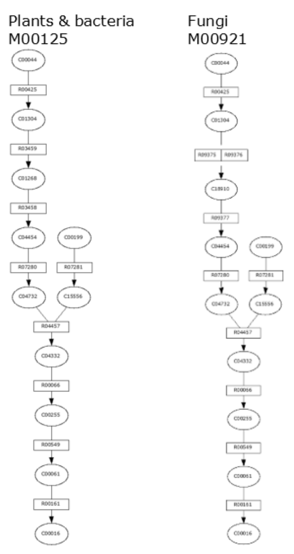
element deficiencies are common in farm soils, especially Mg and Zn (Huettl, 1993; Alloway, 2008; Guo *et al.*, 2016), farmers rarely add these elements. Soil deficiencies likely provoke complex adaptations throughout the food web, from the composition of the microbiome, to altered gene regulation in plants and animals, to overeating of macronutrients driven by "hidden hunger" for deficient trace nutrients. Gene-environment interactions affect crop yields and the mineral and trace element composition of some plant species (Yang *et al.*, 2018) or ionome (Salt *et al.*, 2008). However, GxE effects on nutrient density and food quality are not well studied.

The Kyoto Encyclopedia of Genes and Genomes (KEGG) pathway and Brenda enzyme databases (Kanehisa, 2000; Schomburg *et al.*, 2002) contain information on trace element cofactors for vitamin synthesis, potentially linking crop vitamin content to soil chemistry. We traced each step in the biosynthetic pathway descriptions from KEGG to Brenda and observed metal ion cofactor requirements for the biosynthesis of vitamins A; B1, 2, 3, 4, 6, & 9; C; E; and K & K2. The data on preferred and alternative metallic cofactors often showed that one divalent cation yields the most efficient enzyme performance, but other divalent cations can substitute. For instance, Mg^{++} may be "required", but Fe^{++}, Mn^{++}, Zn^{++}, Co^{++}, Ni^{++}, Cd^{++} or even Pb^{++} may confer some activity. Vitamin synthesis pathways also may include reactions catalyzed by enzymes that require a second vitamin (or even the target vitamin). The synthesis of the secondary vitamin may depend on a cation that is otherwise not required for the synthesis of the first vitamin, so that synthesis of the first vitamin depends indirectly on the cation. However, Brenda records describe human pathogens more often than crops or symbiotic fungi, and the curated data are largely from *in vitro* studies.

The figure illustrates 7 steps in riboflavin synthesis, and an additional 2 steps to reach FAD. The first step "requires" Mg, but the few available reports do not appear to have searched for potential alternative cations. The second and third steps are different in fungi compared to plants and bacteria. The Brenda database indicates that the enzyme in the second plant step contains Zn without describing any dependence. The third fungal step was not linked to any record in Brenda. Otherwise, the enzymes and cofactor requirements are known and similar. Mg ions are preferred in 4 steps leading to riboflavin and preferred in some species for the two steps leading to FAD. Zn ions are involved in 3 steps leading to riboflavin and are preferred in some species for the steps leading to FAD. Manganese and other divalent cations imperfectly substitute for Mg in the late steps in riboflavin synthesis. Although a subsequent critique (Farnham and Grusak, 2014) calls for stronger evidence to support the claim that crops' nutrient density is falling over time, and most inferred declines are modest, one of the largest declines has been in riboflavin (Davis *et al.*, 2004). These observations support the hypothesis that progressive soil Mg or Zn depletion could explain decreasing riboflavin content in crops.

This is the theoretical basis for expecting soil levels of specific divalent cations to correlate with specific vitamin content in crops: Documented vitamin synthesis pathways nearly always include steps catalyzed by enzymes that require a divalent metallic cofactor. Under *in vitro* conditions, Mg^{++} or Zn^{++} is often the best cofactor currently known. Whether this is true *in vivo* is uncertain. Nevertheless, this suggests that soil mineral depletion could reduce crops' vitamin-related food quality.

We can imagine ways that crops could adapt to shortages of preferred divalent cation cofactors that sustain and/or degrade food quality. Plants might be able to shuttle preferred cations between critical vitamin synthesis steps, preserving crops' vitamin content despite declining trace element content. Plants might use toxic alternative divalent cations, like cadmium or lead, as cofactors when preferred cations are deficient, preserving crops' vitamin content while adding harmful elements. In a finding consistent with this hypothesis, we have observed heavy metals appearing in some crops grown with conventional NPK fertilizers, but not in comparison crops grown in regenerative organic soil supplemented with multiple trace elements (Sumner, 2021). Although fungi are not known to provide vitamins to plants, fungi can provide hormones (Gutiérrez-Mañero, 2001) and ergothioneine, a vitamin-like amino acid (Borodina *et al.*, 2020), and bacteria can provide thiamine



Reaction —> product	Enzyme number	Mg	Zn	Alt 1	Alt 2	Vit
R00425	3.5.4.25	R	R	Ø	Ø	Ø
R03459	3.5.4.26	Ø	C	Ø	Ø	Ø
R009375 R009376	1.1.1.302	Ø	Ø	Ø	Ø	NAD
R03458	1.1.1.193	Ø	Ø	Ø	Ø	NAD
R09377	-	-	-	-	-	-
R07280	3.1.3.104	P	Ø	Fe^{++}	DC	Ø
R07281	4.1.99.12	P	S	Mn	DC	Ø
R04457	2.5.1.78	P	Ø	Mn	DC	Ø
R00066 —> Riboflavin	2.5.1.9	P	Ø	Mn	DC	Ø
R00549 —>FMN	2.7.1.26	PL	PL	Mn	DC	Ø
R00161 —>FAD	2.7.7.2	P	PL	Mn	DC	Ø

Figure 1: Plant, bacterial, and fungal biosynthetic pathways for riboflavin (KEGG database) identify compounds in ovals and reactions in rectangles. Reactions are catalyzed by enzymes with a 4-digit identifier in KEGG and Brenda. Brenda includes cofactor observations. C =enzyme contains ion with no further information; DC = various divalent cations confer some activity; NAD = NADH or NADPH required; P = preferred; PL = preferred in limited number of species; R = required, no reported alternatives at present; S = structural component rather than catalytic cofactor; ø = no requirement noted; - = no information on the enzyme.

to fungi (Abeysinghe *et al.*, 2020). There may be conditions in which farm soil microbiomes can synthesize vitamins for a crop, preserving its vitamin content without requiring it to accumulate toxic metals. Research on preferred *in situ* cofactors and potential substitutions in crops, soil mineral content correlations with crops' essential nutrient content, and rhizosphere symbioses on farms with different soil management regimes has potential to improve food security and quality.

Conclusion

Depletion of minor and trace elements, critical cofactors for many enzymes involved in the biosynthesis of nutrients, such as magnesium and zinc is common in many farm soils. Genome wide association studies link common human diseases to genes that encode enzymes that require specific minor and trace elements and vitamins as cofactors. In a depleted environment, crops might respond to a soil mineral deficit by accumulating alternative toxic cations or by reducing biosynthesis of some nutrients. As a result, people eating crops from depleted soils might experience mineral and vitamin deficiencies manifesting as common chronic diseases and in addition experience hidden hunger, and toxicity.

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