Micronutrients and Soil Microorganisms in the Suppression of Potato Common Scab

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Abstract: Nature-friendly approaches for crop protection are sought after in the effort to reduce the use of agrochemicals. However, the transfer of scientific findings to agriculture practice is relatively slow because research results are sometimes contradictory or do not clearly lead to applicable approaches. Common scab of potatoes is a disease affecting potatoes worldwide, for which no definite treatment is available. That is due to many complex interactions affecting its incidence and severity. The review aims to determine options for the control of the disease using additions of micronutrients and modification of microbial communities. We propose three approaches for the improvement by (1) supplying soils with limiting nutrients, (2) supporting microbial communities with high mineral solubilization capabilities or (3) applying communities antagonistic to the pathogen. The procedures for the disease control may include fertilization with micronutrients and appropriate organic matter or inoculation with beneficial strains selected according to local environmental conditions. Further research is proposed to use metagenomics/metabolomics to identify key soil–plant–microbe interactions in comparisons of disease-suppressive and -conducive soils.

Keywords: micronutrients; mineral solubilization; inoculation; suppressive soils; antagonistic strains

1. Introduction

At present, both agriculture science and management seek to understand ecological processes which are relevant to the control of plant diseases [1,2]. New findings are expected to diminish the use of agrochemicals, which decrease the biodiversity of non-target organisms, including microbial communities in agroecosystems [3]. Proposed approaches focus on biological protection, mostly using microorganisms supporting plant growth and health [4]. However, more traditional approaches can also be used. One of the well-studied mechanisms of plant protection concerns providing plants with sufficient resources/nutrients such as nitrogen, phosphorus or potassium but also trace elements [5]. Many agricultural soils are deficient in one or more nutrients, and the production of crops depletes, particularly, micronutrients, because macronutrients are typically supplied in high amounts [6]. That leads not only to suboptimal plant growth but also to decreased plant immunity, which is influenced by their metabolic status [7,8]. Thus, composed plant nutrition is critical for disease control. That is because a delicate balance between the specific nutrient requirements of various potato cultivars and the soil chemical conditions need to be established [9–14].

Common scab (CS) is a disease potentially affected by plant mineral nutrients [15]. Previous studies associated nitrogen, phosphorus, potassium, calcium, magnesium, iron, zinc, manganese, copper and aluminum with CS severity or incidence by their content

either in soil or plant tissue [15–17]. The use of nutrients to control CS was investigated but the effects differed by location, cultivar and year [16–21].

The second studied mechanism of disease control involves plant–microbe–soil interactions, which include (1) antibiosis; (2) competition with pathogens, (3) induction of systemic defense response, (4) plant growth promotion and also (5) increased availability of nutrients, which all affect plant defense [22]. It was suggested that, particularly, the soil [23] and potato plant microbiomes [24,25] are important in controlling plant diseases.

Common scab of potatoes (CS) is a disease caused by pathogenic *Streptomyces* spp., which are distributed worldwide and, thus, adapted to various soil conditions [26]. In the past, the disease was treated by several pesticides, e.g., formaldehyde, urea formaldehyde, manganese sulphate, pentachloronitrobenzene and chloropicrin, whose use is now limited. In spite of increased research efforts, no treatments provide a reliable control of the disease across locations [26].

Most of the generally known microbial activities connected to plant disease control were also observed in CS-related interactions, particularly in suppressive soils [27–30]. Extensive research was conducted with supplementation of antagonistic strains to soil or improvement of the whole microbial communities using organic substrates reviewed in [31]. Above that, many cases of pathogen suppression by the microbial community were also related to the soil nutrient status [32,33]. Yet, no conclusive results useful for disease management were determined.

Consequently, in this review, we combine the chemical, physiological and microbiological research concerning CS to uncover the underlying processes which could be used for disease control. We focus on the effects of micronutrients because their sufficient amount is required for many physiological processes which support the defense against plant diseases. Additionally, micronutrient availability is relatively easy to manage [6]. We also recognize that microorganisms are integral components of soils, and therefore, their participation in potato plant nutrition and protection against CS needs to be considered in disease control. Finally, we recommend approaches for the most appropriate management strategies.

2. Individual Nutrients Affect CS Severity

Potatoes require optimal levels of essential nutrients throughout the growing season. Therefore, disease severity may be influenced by nutrient limitation, particularly at periods of fast growth [34]. Potato plants respond to the presence of the CS pathogen and nutrient conditions by accumulating various macro- and microelements. A significant correlation was shown between the degree of infestation by CS and the contents of Ca, Mn, K, P, Fe and Mg [15–17,35] in potato periderm or other parts of plants. The ability to accumulate different macro- and microelements also differs between cultivars and is further associated with resistance to CS [36]. However, it seems that the accumulation of different nutrients in potato periderm results from various processes, and thus, only some interactions are indicative of CS effects or can be used for its suppression.

2.1. Micronutrients

2.1.1. Calcium (Ca)

Ca relationships to CS are some of the most studied, in combination with soil pH. High total calcium levels in soil and also composed exchangeable Ca are often positively correlated with CS severity [17,27,28,37]. However, addition of Ca and K to acidic and neutral soils increased CS severity only in the neutral soil, showing that pH and Ca:K ratio are more important than the content of Ca in soil alone [38]. Similarly, the irregular relationship between soil pH, exchangeable Ca and CS development (e.g., [35]) was explained by interactions with other nutrients, including phosphorus, nitrogen and manganese [17,39] (Table 1).

Limitation of plant growth is relatively unlikely with Ca because it is a component of several primary and secondary minerals and is commonly present in ionic form (positively charged Ca^{2+}), which is considered biologically available. Limitations may occur when

it is adsorbed on soil colloidal complexes or due to human-induced acidification of soils, when Ca deficiency is caused by antagonistic plant uptake of metals such as aluminum, potassium and manganese [5,40].

However, limited Ca uptake influences the disease development because in plants, Ca affects the stability and function of membranes and cell wall structures [5,40,41]. Furthermore, Ca serves as a second messenger triggered by different environmental stimuli, including pathogens, so it is needed for plant defense [40]. In CS lesions, the Ca level is elevated [42] and it is even higher in dry soil conditions [43]. Thus, the high Ca level in the tuber periderm of diseased plants [36] shows an effect of infection rather than a cause [35]. However in healthy potatoes, a positive correlation between the Ca content and CS severity suggested that susceptible cultivars accumulate higher amounts of Ca [44].

Consequently, the total Ca content in the soil does not seem to be a good predictor of CS disease because it interacts with many other soil nutrients, pH and soil moisture and is affected by potato plant genetics. However, occasional liming of low-pH soils is recommended for prevention of Ca limitation, which also leads to increased disease severity. Above that, manipulation of soil Ca leads to fluctuations in soil pH, which may further improve CS prevention because different pathogenic streptomycetes are adapted to specific soil pH levels, and thus, its decrease or increase may suppress their populations [15,45]. In contrast, the selection of cultivars which accumulate lower amounts of Ca in the periderm may be a good strategy for CS control (Table 1).

2.1.2. Sulphur (S)

The application of elemental sulfur, calcium sulfate and ammonium sulfate reduced CS infection and severity [46,47], and above that, sulfate fertilizers enhanced biodiversity and antibiosis [46,48]. CS severity was also negatively correlated with soil S content [32]. Yet the effect of elemental sulfur and ammonium sulfate on the reduction in CS was not consistent [47].

Sulfur availability in soil depends highly on soil bacteria because more than 95% of total sulfur is bound to organic molecules in the form of sulfate esters or carbon-bonded sulfur (sulfonates or amino acid sulfur). Bacteria participate in both the formation of those compounds (sulfur immobilization) and sulfur release in the form of sulfate, which is available to plants [49]. Additionally, different microbial communities are involved in the consumption of various sulfur sources and supplying of sulfur to potato plants [50].

In the plant, organically bound sulfur in the form of various sulfur-containing metabolites is involved in cellular self-defense processes including detoxification of reactive oxygen species and other redox reactions, collectively termed sulfur-induced resistance or sulfur-enhanced defense [51]. Additionally, sulfur deficiency also has an indirect effect on plants as it reduces uptake of other elements such as P and K [40,52]. To improve CS control, it seems that the increase in decomposition processes by priming with additions of new organic matter may lead to the release of S from older soil organic matter and support microorganisms increasing S availability.

2.1.3. Magnesium (Mg)

In several studies, CS decreased and no pathogen (*Streptomyces scabiei*) was detected on potatoes grown in soils with high composed exchangeable cations including Mg [37]. Similarly, CS-suppressive soils were enriched in total Mg compared to CS-conducive soils [27]. A connection of Mg and CS suppression was also found in a resistant potato cultivar that also had a higher Mg content in the periderm compared to a susceptible cultivar [28]. However, in another study, the number of thaxtomin gene copies (*txtB*) representing the quantity of the pathogens in potato periderm was found positively correlated to periderm Mg content [32].

Mg availability in soil depends on soil weathering, moisture, pH and root–microbial activity, which are key factors determining the plant-available Mg pool [53]. Yet Mg is usually not limiting because it is present in various types of silicates and is relatively mobile

compared to other cations such as K, Ca and NH_4^+ [54]. However, similar to other cations, deficiency of Mg^{2+} in the plant may be induced not only by its low soil content but also by other cations that compete with Mg^{2+} for binding to negatively charged clay particles or root apoplasm [55].

Magnesium is an important co-factor of more than 300 enzymes [53], including RuBisCO, a central part of a chlorophyll molecule [40], and also functions as a carrier of phosphorus in plants. Nevertheless, excess Mg^{2+} may also inhibit photosynthesis, particularly during dehydration [56] (Table 1).

Thus, for improvement of Mg-related limitation of plant growth and health, mostly a selection of cultivars with better Mg utilization may be recommended [44] or, in case of larger limitation, soil can be supplemented with dolomite, the most common Mg fertilizer.

2.1.4. Manganese (Mn)

High Mn content (Mehlich 3-extractable) was strongly correlated with low CS disease severity of soils in Canada [16]. Soil amendments which reduced Mn availability such as liming and nitrate fertilizers also increased the severity of CS [57]. Furthermore, direct Mn soil applications reduced the common scab of potato, especially when manganese sulfate was applied to Mn-deficient soils [58]. However, Barnes [59] found no effect on CS incidence when up to 125 kg/ha of $MnSO_4$ was applied on tubers or sprayed at tuber initiation (Table 1).

The availability of manganese depends on soil acidity. However, in soil, not only may limitation occur, but sometimes, a level toxic to plants was observed at some locations [57,60,61]. Yet more often, Mn is deficient, and that is connected with the increasing severity of various plant diseases.

In the plant, Mn serves as a co-factor of various enzymatic activities at low concentrations, while at high concentrations, it acts as their inhibitor [57]. Above that, Mn deficiency leads to an inhibition of cell elongation and decrease in tuber yield [61]. Thus, Mn limitation not only affects the overall growth of plants but also the thickness of the cell wall, which serves as protection for pathogen invasion [6]. Finally, Mn may affect the disease resistance of plants by controlling lignin and suberin biosynthesis, phenol biosynthesis and photosynthesis [5,41,62].

Limitation of Mn may not be related only to its availability in soil. Since Mn is required at much higher concentrations by higher plants compared to fungi or bacteria, some pathogens are known to exploit this difference in requirement [63]. For example, some plant pathogens, including *S. scabiei* oxidize Mn, making it unavailable for the plant host and, thus, increasing the plant stress [64].

Consequently, Mn limitation may strongly affect disease control and should be assessed when macronutrients are in balance. The form of supplementation might be evaluated based on soil pH and organic matter content because both inorganic and organic forms can be applied for the improvement of Mn availability. Some organic amendments such as dried grass meal may also increase the number of manganese-reducing microorganisms [65] which make manganese available to plants.

Table 1. Mineral nutrients availability in relation to common scab (CS) development.

Element	Factors of Availability to Plants	Function in Plant	Relation to Plant Defense/Pathogenesis in General	Possible Relation to CS	Main References
Cation Exchange Capacity (CEC)	Higher CEC in clay than sandy soils; low CEC and Ca especially correlated with low pH	A measure of soil capacity to hold nutrients (Ca, Mg, K, Na, Al and H)	Different effects of Ca, Mg, K and their ratio; imbalanced nutrients promote impaired biosynthesis and accumulation of low-molecular weight substances readily available for parasites	CS disease severity related to exchangeable Ca, Mg and K cations; CEC is lower in suppressive soil; the higher CEC, the greater uptake of Ca^{2+}; uptake of monovalent cations (K^+) increases at lower CEC	[5,37,60,66]
K	Leached out in acid soils; Al dominates the CEC, limits the soil's ability to absorb and hold K	Control of cation–anion homeostasis, membrane polarization, more than 60 enzymes in photosynthesis and transport of photosynthetic products to storage organs; starch synthesis; increased plant resistance to pests, diseases and abiotic stresses	Correlated with K:Mg, K:Ca and K:N ratios; decrease in some plant diseases if N and P are sufficient; high content of N increases plant susceptibility to diseases—this adverse effect can be neutralized by balanced N:K ratios of fertilizers	Special Ca:K ratio reduces scab severity and incidence, while the imbalance or excess of K or Ca promotes the disease	[38,40,64,66]
Ca	pH	Stability and function of membranes and cell walls; second messenger triggered by different stimuli including pathogens	At low Ca level, cells leak compounds used as food by parasites; supports some pathogens by stimulating the action of pectolytic enzymes dissolving plant cell wall; inhibits the activity of other pectolytic enzymes	Ca may simulate the aerial mycelium formation and spore germination of *S. scabiei;* high calcium levels in the absence of changes in pH induce scab	[35,40,41,66]
Mg	Mg deficiency can be induced by higher K supply	Allosteric activator of more than 300 enzymes; a central part of chlorophyll molecules; in the structural integrity of cell components	Decreases the susceptibility to pathogen-produced macerating enzymes as long as Ca level remains sufficient	Soils suppressive to CS disease had a higher content of Mg; the CS-resistant potato cultivar has a higher Mg content in periderm	[27,28,40,53]

Table 1. *Cont.*

Element	Factors of Availability to Plants	Function in Plant	Relation to Plant Defense/Pathogenesis in General	Possible Relation to CS	Main References
Mn	More available with lower pH; Mn uptake increased by seed inoculation with pseudomonads, organic amendments increased Mn-reducing microorganisms	Co-factor of enzymatic activity/an inhibitor at high concentrations; control of lignin and suberin biosynthesis, phenol biosynthesis, photosynthesis	Mn is required at much higher concentrations by higher plants than by fungi and bacteria	High Mn correlates with low CS; *S. scabiei* oxidize Mn making it unavailable for the plant; soil amendments reducing Mn availability (liming, nitrate fertilizers) increase CS severity; herbicide glyphosate, toxic to Mn reducing organisms	[55,57]
Fe	Predominant ferric ion (Fe^{+3}) is sparingly soluble; more available at lower pH as reduced form Fe^{+2}; bacteria supply iron to plants and backward	DNA synthesis, respiration, photosynthesis; in prosthetic groups of many enzymes (cytochromes); synthesis of chlorophyll; essential for maintenance of chloroplast structure and function	Plants, bacteria and fungi compete for Fe in the rhizosphere; microorganisms have lower Fe requirements than plants; promotes antifungals' production by soil bacteria for plant benefit; activates both enzymes involved in the infection and in plant defense	*S. scabiei* produces siderophores desferrioxamine, scabichelin and pyochelin to compete for iron; lower CS severity in soils with more available iron; higher Fe in the periderm of tubers grown in suppressive soil; enrichment with available iron and peat suppressed CS	[5,27,33,67–70]

2.1.5. Iron (Fe)

In CS-suppressive soils, potatoes were less affected due to the available iron [33]. Furthermore, the concentration of Fe in the periderm of potato tubers grown in CS-suppressive soils significantly increased during the maturation period, whereas in conductive soils, it slightly decreased [36]. Overall, although cultivars differ in Fe requirements [71], the Fe content in various cultivars was usually not related to the CS disease [44]. Finally, the enrichment of soil with soluble iron (directly or through a decrease in soil pH by peat amendments) suppressed the CS severity, although the abundance of thaxtomin biosynthetic gene copies (*txtB* genes) remained the same in the soil. This indicates that iron supports plant defense and reduces pathogen virulence rather than eliminating the pathogen population [27,33] (Table 1).

Although iron is the fourth most abundant element on Earth, it is not readily assimilated by either bacteria or plants in aerobic soils because its oxidized form, Fe^{3+}, is only sparingly soluble. Plant availability of Fe is also greatly reduced in calcareous soils (pH > 7) [7]. That is in contrast with requirements of high iron levels by both microorganisms and plants. It is particularly problematic in the rhizosphere, where plants, bacteria and fungi compete for it [69]. Plants have developed two strategies for iron uptake: (1) mostly dicots acidify the rhizosphere by the production of organic acids and phenolic compounds to activate ferric chelate reductase and Fe^{2+} transporters; while (2) monocots produce phytosiderophores and respective transporters [69]. Bacteria have developed similar strategies of producing organic acids and synthesizing low-molecular-mass siderophores (~400–1500 Da), molecules with a high affinity for Fe^{3+} as well as membrane receptors able to bind the Fe–siderophore complexes [72]. Many plant pathogens, including *S. scabiei*, use chelating compounds during iron uptake, and those can act as essential virulence determinants by limiting the plant's access to iron. *S. scabiei* produces three types of siderophores: desferrioxamine, scabichelin and pyochelin [73,74] (Table 1).

The effect of iron deficiency is critical for plants in metabolic processes such as DNA synthesis, respiration and photosynthesis because it serves as a co-factor of many enzymes, such as cytochromes of the electron transport chain. It is involved in the synthesis of chlorophyll and is essential for the maintenance of chloroplast structure and function [67]. Additionally, iron may participate directly in the activation of enzymes involved in infection as well as those involved in plant defense [75]. In addition, the availability of iron is important for the protective microbial community because it is required for the production of biocontrol metabolites, which may suppress various diseases [22].

The availability of iron seems to be the most overlooked factor in the protection of potato plants from different diseases, but particularly CS, because the pathogenic streptomycetes are well equipped for competition with the plants for iron supplies. The deficiency is likely in all alkaline soils but also in soils with low microbial activities. Thus, the availability of iron can be improved by supplementation with organic matter which increases microbial activities but also by fertilization by organically bound iron.

2.2. Macronutrients

Even though macronutrients are not in the main focus of CS disease control, nitrogen, phosphorus and potassium are often limiting factors and have also been demonstrated to affect CS severity, despite their regular amendments to arable soils. Similarly to micronutrients, particularly their balanced soil contents and availability are important because of many common interactions [5].

2.2.1. Nitrogen (N)

Most soils are poor in nitrogen, so it is generally supplied; yet its local recycling is often overlooked. The soil nitrogen pool is mostly replenished by ammonium released from dead biomass by microbial decomposers in natural conditions [76,77] and from the atmosphere by nitrogen fixation by symbiotic bacteria [78] or free-living bacteria and archaea [79]. The processes are attenuated by fertilizers containing large amounts of nitrogen. To

understand local nitrogen status, the proportion of ammonia-oxidizing bacteria to archaea in the rhizosphere represents a potential bioindicator because it correlates with soil health status [80]. In addition, nitrogen-rich rocks occurring at some locations should not be overlooked because they offer a potentially large pool of nitrogen, and thus, no fertilization is required [81].

In CS, some studies showed that adding N-rich soy meal, meat and bone meal to soil led to an increase in ammonia, nitrite, nitrate, pH and bacterial quantity and suppressed CS [82]. Furthermore, the temporary initial increase in soil pH to eight or higher by the addition of organic materials resulted in an increase in free ammonium levels that might be toxic to populations of *S. scabies* [83]. It was also shown that oligotrophic conditions of low soil C and N are associated with CS control, possibly because the low N content constrains the pathogens, favoring copiotrophic soil conditions [27].

The observed differences in nitrogen's impact on CS may be the result of a partially different utilization by potato cultivars [84]. A high content of N is known to increase the plant susceptibility to several diseases, but the adverse effect can be neutralized by balanced N:K ratios of fertilizers [66].

Thus, soil N content should be checked for balance with other nutrients, and fertilization by nitrogen should be evaluated carefully for CS control so as not to eliminate microbial activities. Furthermore, ammonium levels may be important indicators of microbial processes relevant to CS control.

2.2.2. Phosphorus (P)

The relationship of soil P to CS has been studied for a long time. Recently, a high soil phosphorus content was observed in CS-suppressive fields [27], and CS severity was negatively correlated with the total phosphorus content in both soil and potato periderm [32,44]. Similar to other nutrients, there is a combination of the nutrient's effects on the plant and the pathogen, which need to be disentangled to suggest an appropriate strategy for CS control.

Ecosystems begin their existence with a fixed amount of P, which cannot be readily replenished. Consequently, ecosystems with very old soils can become P-limited [2]. P in soil is subject to an extensive set of physico-chemical and biological reactions, while only a small part of total soil P is in a biologically available form [85]. In particular, in calcareous soils, precipitation of calcium phosphate is presumed to be a major factor in the loss of P availability over time [86]. As one of six macroelements, phosphorus is directly involved in all processes in the plant. Additionally, potatoes have a relatively high P requirement but are rather inefficient in soil P uptake [34], so deficiency is likely to occur.

In the plant, phosphorus deficiency results in a broad range of stress and adaptation responses [87], including changes in the root system morphology and increased expression of phosphoenolpyruvate carboxylase, resulting in root exudation of organic acids, which changes P equilibrium in the plant rhizosphere and may influence the development of specific microbial groups, including pathogens [88]. Similarly, phosphate-solubilizing microorganisms, e.g., the genera *Bacillus*, *Pseudomonas*, *Agrobacterium*, *Acetobacter*, *Streptomyces* and *Nocardia*, release P from parent rocks and other sparingly soluble forms of soil P by secreting organic acids, and during the process, they decrease the particle size [66]. Yet, microbial communities differ by P release, possibly also due to a pressure by predators, which speeds up its recycling. This was suggested as a partial mechanism in some disease-suppressive soils [14].

However, it was observed that the content of available soil P is related to the amounts of carbon, lignin, cellulose, polyphenol and nitrogen. For this reason, their quantities may be used as predictors of the P release in various soils [86].

To assist the optimal P levels for CS disease control, solubilization activities by microorganisms can be supported by an increase in organic matter, particularly if it is slightly acidic. Selection of potato cultivars with higher capacity of P uptake is also recommended because potato cultivars vary in the efficiency of P utilization [44].

2.2.3. Potassium

Potassium has the highest concentrations in potato tubers out of all macronutrients [40, 62] but the impact of its content on CS varies greatly. Potassium concentration measured in the tuber periderm was not related to CS occurrence or severity in various potato cultivars [36]. Yet in other studies, CS severity positively correlated with the available soil K content [16], and CS was less severe in soils with a relatively high concentration of exchangeable Ca, Mg and K [37].

The sources of potassium are minerals—feldspars and micas—which release this element in the course of their weathering. Weathered potassium appears in solution as an exchangeable ion, K^+, which is adsorbed to or released from surfaces of clay particles or organic matter [89]. Therefore, the presence of K-rich minerals and soil clay content needs to be considered before its supplementation. Similar to other nutrients, K-solubilizing microorganisms assist its availability, so their enrichment may benefit plants in soils where K is present but not in forms available to plants [90].

Similar to other macronutrients, potassium in plants controls major pathways such as cation–anion homeostasis, membrane polarization and enzymatic activity [40]. K is also involved in more than 60 enzymes participating in photosynthesis, moving photosynthetic products to storage organs such as seeds and tubers [66] and starch synthesis [40]. K plays an important role in increasing plant resistance to pests, diseases and abiotic stresses [66]. Its deficiency leads to impaired synthesis of high-molecular-weight compounds (proteins, starch and cellulose), while low-molecular-weight organic compounds accumulate and are easily available to the invading plant pathogens [5].

Potassium's equilibrium with other macronutrients is particularly important for the prevention of CS. However, cultivars with a higher K uptake may be also selected to prevent K limitation because various cultivars differ strongly in K accumulation [44].

3. Organic Matter Modifies Microbial Communities and Increases Antibiosis

The application of organic amendments to soil was proposed as a strategy for the management of diseases caused by soil-borne pathogens [91]. Soil organic matter (SOM) supplementation can produce suppressive soils on which pathogens do not establish or persist [92,93]. Though many attempts have been made to suppress various plant diseases, they have generally been met with varied success [91,94].

Many studies showed also CS reductions with the addition of various organic materials, including compost [95], peat [33], green manure [92,96], several types of animal manure [83,97,98] and fish emulsion [21] (Table 2). Although the effect of organic amendments was found to be mostly beneficial, rarely were the causes for the observed effects on CS (intensification or suppression) resolved. It seems that the results depend on the organic matter quality but also on the period and frequency of application [98,99]. Therefore, a more precise understanding of organic matter supplementation is needed for successful CS control.

Currently known mechanisms of SOM impact on the development of plant diseases include (1) decrease in soil pH and increase in nutrient availability [100], (2) improvement of soil nutrient-holding capacity and stability [101] and (3) disease-suppressive activities of soil microbial communities [22]. Regarding CS specifically, direct suppression of the pathogen *S. scabies* by harmful organic compounds was achieved by fertilization with chestnut waste [102]. Finally, the connection between CS severity and SOM content may be explained by the preferential food hypothesis, according to which carbon substrate-deprived *Streptomyces* develop a pathogenic tendency, while their usual lifestyle is benign and saprophytic [103].

Table 2. Effects of organic matter amendments on incidence and severity of potato common scab.

Material	Quantity	Method	Effect	Reference
Compost	0.4 mt ha^{-1}		CS suppression 42%	[95]
Aerobic compost tea	140 L ha^{-1}	Back-pack sprayer	CS suppression 81%	
Indian mustard green manure		In the year before potatoes	CS suppression 25%	[96]
Barley/ryegrass rotations		Rotated prior to potatoes	CS suppression 13–34%	[104]
Lopsided oat (*Avena strigosa*)	150 kg ha^{-1}	Rotovator prior to potatoes	CS suppression	[105]
Rice bran	3 t ha^{-1}	In the furrow with the seed tubers	CS suppression (DS)	[106]
Soybean green manure, with wheat straw		Incorporated before planting	CS suppression	[107]
Green manure (*Brassica napus*)		Grown for approx. 2 months in the fall	Decrease in CS incidence and severity	[92]
Compost	2.5 kg m^{-2}	5 days before planting	CS suppression: 61% to 28% DI, 30% to 16% DS [a]	[108]
Compost tea	1 kg m^{-2} in 5 L water	Soil drenching	CS suppression: 61% to 32% DI, 30% to 15% DS	
Fish emulsion	1%	Soil amendment	No effect	[21]
Processed swine manure	2 g per seed	Seed covering	Increased DI	[109]
Processed swine manure with chitosan	2 g per seed; 1% chitosan	Seed covering	no effect	
Chicken manure	66 t ha^{-1}	Incorporated to 15-cm depth	CS suppression	[83]
Swine manure	5.5 m^3 ha^{-1}		CS suppression	
Dairy cattle manure	100 t ha^{-1}		No effect	
Poultry manure	1.54–12.32 Mg C ha^{-1}	Applied dehydrated, pelletized prior to planting potatoes	CS suppression	[98]
Poultry manure, forestry residues and organic waste compost	45 Mg ha^{-1}	Incorporated to a depth of 15 cm in October, a year before planting	CS suppression	[97]
Meat and bone meal	37 t ha^{-1}	Incorporated to 15-cm depth	CS suppression	[16]
Soymeal	37 t ha^{-1}		CS suppression	
Poultry manure	66 t ha^{-1}		CS suppression	
Poultry manure	20 t ha^{-1}		No effect	
Nature Safe 10-2-8 (poultry feathers)	10 t ha^{-1}		CS suppression by 50–100%	
Ammonium lignosulfonate	1000 L ha^{-1}		Marketable yield 60–80% compared to 10% in the control	
Peat	2.5 L peat /10 L soil	In submerged pots	CS suppression	[33]

[a] DS—disease severity (percentage of surface covered with lesions); DI—disease incidence (proportion of infected tubers).

Green manures seem to particularly affect the availability of nutrients such as P, Mn and Zn, which are related to plant defense [91,110]. The application of peat or other low-N, low-pH SOM may also result in solubilization of nutrients, particularly Fe, but also other metals. The additions of low-pH SOM can be also followed by shifts of microbial community composition towards the increase in suppressive activities [33,91]. Green manures combined with appropriate crop rotation may also increase the protective streptomycetes soil sub-community [5,104,111].

Soil suppressiveness reinforced by activities of microbial communities was observed after addition of older compost, aerobic compost tea [95], decomposed wheat straw or soybeans [107], lopsided oat [105] or rice bran [106]. Those manipulations were later connected to increased lignin content, which can induce the production of secondary metabolites controlling the pathogen [112].

As efficient soil saprophytes, streptomycetes are especially likely to respond to the incorporation of organic material into the soil and are often implicated as microbial agents responsible for amendment-induced suppression [106,113]. This was demonstrated by organic amendments, which enriched, especially, some *Streptomyces* populations [113,114], but also with actinobacteria isolates derived from the rice bran-amended soil, which showed antagonistic activity against pathogenic *S. scabiei* and *S. turgidiscabies* [106] (Table 2). However, the use of antibiotic-resistant *S. scabies* mutants indicated that some streptomycetes strains can reduce pathogen populations even when they are not sensitive to antibiotic inhibition. It demonstrated that competition by non-pathogenic streptomycetes for space and resources rather than antibiotic activities efficiently eliminates *Streptomyces* pathogens by competitive exclusion. Thus, both antibiotic inhibition and competition between pathogenic and non-pathogenic *Streptomyces* are likely to be important mechanisms of natural suppression of potato scab [29].

In contrast, increased CS severity and/or incidence was observed after fertilization with fresh animal manure but also with compost [91,99]. In another study, CS-suppressive and -conducive soils were discriminated by specific low-molecular-weight organic compounds [27,115]. Finally, in the same study, the quantity of CS pathogens (thaxtomin biosynthetic gene *txtB* copies) was positively correlated with the soil total C and N contents, whose proportion approximates the type of SOM and its degradability by soil microorganisms [27].

It was suggested that CS pathogens can persist in soil for many years, surviving on decaying plant debris, especially where heavy loads of animal manure were applied [116], and that they possibly survive there by feeding on oligosaccharides released by ligninolytic and cellulolytic microorganisms [117,118]. This "cheating" behavior of CS pathogens suggests that competitive relationships may occur between them and ligninolytic or cellulolytic streptomycetes. The intensity of the competition might be dependent on the quality of available SOM [29,112,114]. Some of these oligosaccharides also act as environmental signals to plant pathogenic *Streptomyces* inducing the production of thaxtomin [117] so that they may further support their pathogenicity, but the regulation of those pathways is not completely resolved [119].

The inconsistent effects of various SOM additions on CS severity and incidence together with the knowledge on the importance of different carbohydrates in the induction of specific metabolic pathways in both pathogenic and beneficial streptomycetes suggest that a more precise SOM characterization is needed in future research, because only gross measurements have been provided for field testing so far [115]. Thus, we propose that organic matter supplements containing oligo- and monosaccharides should be avoided, while fresh low-pH SOM will help in nutrient release, and older, more decomposed SOM will benefit activities of antagonistic streptomycetes.

4. Rhizosphere Microorganisms Influence Nutrient Recycling and Produce Beneficial Metabolites

Microbial communities of the crop rhizosphere are essential not only for plant nutrition and health but also for nutrient cycling in agroecosystems. Therefore, there is a need to link

soil properties, especially the content and character of organic matter, with the distribution and activity of microorganisms and their use in plant protection.

Soil type and pH exert the most profound influence on the structure and function of bacterial communities [120]. In the rhizosphere, microbial communities are additionally shaped by the plant through its root exudates [121–124]. In return, the rhizosphere and also soil-derived endophytic microorganisms support the plant growth, health and metabolism [125]. The main activities of these plant-associated microorganisms are related to recycling of nutrients through mineralization of root exudates, nitrogen fixation or solubilization of minerals. Some microbes may also produce plant hormones and increase root growth [55]. This interaction is particularly important in plant management strategies because the population density of microorganisms in the rhizosphere is several times greater than that in bulk soil [126].

The composition of microbial communities in the rhizosphere is also influenced by the invasion of pathogens, which poses consequences not only for the particular disease but also for the functioning of the whole community [127]. Then, suppressive soils may act differently than conducive soils with respect to microbial community changes [22,28]. Furthermore, the suppressive effect is differentiated between induced suppressive soils of long-term monoculture and natural suppressive soils that undergo regular crop rotation [27,31,128,129].

Induced suppressive soils for CS contained a higher proportion of *Acetobacteraceae*, *Bacillaceae* and *Lysobacter* (*Xanthomonadaceae*) but also non-pathogenic *Streptomyces* (*Actinobacteria*) and lower proportions of some *Acidobacteria*, *Nocardioidaceae* and *Pseudomonadaceae* [130]. The naturally suppressive soils were enriched in *Pseudomonadaceae*, *Bradyrhizobiaceae*, *Acetobacteraceae* and *Paenibacillaceae*, which are all families of known plant growth-promoting microbes [28]. Some of the taxa occurring in suppressive soils were also enriched in soils supplemented with organic matter, which also led to CS suppression. These include *Bacillus*, *Streptomyces* [106] as well as *Solirubrobacteraceae*, *Xanthomonadaceae* and *Sphingomonadaceae* [33] (Table 3).

The suppressivity of soils is not only connected to the bottom-up control of the microbial communities, which is represented by soil physical characteristics [131], contents of nutrients (e.g., [27,33]), production of plant hormones [132] and organic matter quality [97], because the second half of the story is the top-down control by a range of bacterial and eukaryotic consumers and predators. Furthermore, predation by protists is also considered the missing link to understand soil suppressiveness because they are increasingly recognized as an essential component in nutrient recycling, shaping plant physiology, nutrition and health [14]. Those findings come from experiments conducted in controlled environments, where protists could influence the disease-suppressive ability of microbial communities directly by decreasing their numbers or via changes in the community composition [133]. Regarding CS, the micro-eukaryotic community was enriched with *Chlorophyta* together with *Myxogastria*, *Apicomplexa* and *Ciliophora* in CS-conducive soil, which consequently displayed increased micro-eukaryotic diversity and a higher number of putative interactions. Furthermore, micro-eukaryotic community was correlated with soil pH and contents of C, N, P, Ca and Fe in conducive soil but with S content in suppressive soil [28]. Thus, although the results are only preliminary, it seems that not only nutrient cycling and plant nutrition but also disease protection may be affected by trophic relationships [134].

Modification of plant-associated microbial communities can be achieved by planting various cultivars, because their tuberospheres are inhabited by cultivar-specific bacterial communities, which also comply with the cultivars' resistance to CS [28,135]. For example, *Nitrospirae* and *Acidobacteria* were enriched in a resistant cultivar together with a decreased ratio of *Thaumarchaeota/Euryarchaeota*. Out of these, *Nitrospirae* and *Thaumarchaeota* belong among important nitrifiers and ammonia-oxidizers, respectively, which points to their connection with nitrogen cycling. The increase in *Acidobacteria* suggests that a decrease in pH and an increase in *Euryarchaeota* points to the modification of pH, moisture or the carbon cycle [28,136]. In another study, microbial communities associated with resistant

cultivars exhibited lower abundance of bacteria, higher diversity, higher co-occurrence network complexity and increased community functioning.

Table 3. Microbial community changes associated with lowered CS severity due to soil suppressivity, potato cultivar or soil amendment.

Manipulation	Affected Bacterial Groups	Reference
Suppressive soil	Higher frequency of antagonistic pseudomonads and streptomycetes and higher proportion of pathogenic streptomycetes by cultivation; different microbial community by terminal restriction fragment analysis	[137]
Suppressive soil	Higher proportion of *Acetobacteraceae*, *Bacillaceae* and *Lysobacter* (*Xanthomonadaceae*), lower *Acidobacteria* group 6, *Nocardioidaceae*, *Pseudomonadaceae*, unclassified *Acidobacteria* group 11 and unclassified *Bacilli*	[130]
Suppressive soil	Enriched in *Pseudomonadaceae*, *Bradyrhizobiaceae*, *Acetobacteraceae* and *Paenibacillaceae*; decreased ratio of *Thaumarchaeota/Euryarchaeota* in tuberosphere of susceptible cultivar; higher proportions of Ascomycota and Basidiomycota and lower proportions of Chlorophyta, Ciliophora, Myxogastria and Apicomplexa	[28]
Resistant cultivar	Same as in suppressive soil and enriched in *Nitrospirae and Acidobacteria*; decreased tuberosphere ratio of *Thaumarchaeota/Euryarchaeota* in conducive soil; Chlorophyta and Cercozoa in lower proportions	
Resistant cultivar	More non-pathogenic streptomycetes than in susceptible cultivar	[138]
Resistant cultivar	Cloning/Sanger sequencing analysis of root, tuber and rhizosphere bacterial communities of 8 cultivars differing in resistance to CS; higher abundance of *S. turgidiscabies* in susceptible cultivars by qPCR	[30]
Susceptible cultivar	*Variovorax*, *Stenotrophomonas* and *Agrobacterium* were positively, and *Geobacillus*, *Curtobacterium* and unclassified *Geodermatophilaceae* negatively, correlated with the scab severity level, estimated absolute abundance of pathogenic *Streptomyces* and *txtAB* genes	[23]
Biocontrol strain *Pseudomonas fluorescens* LBUM223	Inoculation does not significantly alter the autochthonous rhizosphere nor geocaulosphere microbiomes in the field	[139]
Rice bran amendment	*Bacillus*, *Streptomyces*, *Chitinophaga* and *Actinomadura* significantly increased; unclassified *Koribacteraceae* and unclassified *Gaiellaceae* were significantly reduced	[106]
Iron amendment	*Bacillales* and *Gaiellales*	[33]
Peat amendment	*Rhizobiales*, *Burkholderiales*, *Xanthomonadales* and *Bacillales*	
Peat and iron amendment	*Proteobacteria* and *Bacteroidetes* increased at the proportional expense of *Actinobacteria*; proteobacterial *Burkholderiales*, *Xanthomonadales* and *Sphingomonadales* and actinobacterial order of *Gaiellales* were the most responsive groups; actinobacterial families *Micromonosporaceae* and *Thermomonosporaceae* were elevated	

Furthermore, a metagenomic approach showed that particularly the enrichment of antibiotic biosynthesis pathways within members of bacterial communities was typical for the tuberosphere soil of healthy tubers. In contrast, the tuberosphere soil of diseased tubers was enriched in *Variovorax*, *Stenotrophomonas* and *Agrobacterium* together with several ABC transporter genes, genes of bacterial secretion system, quorum sensing, cytochrome P450 and also genes for nitrogen metabolism [23]. Comparison between the metagenomes differently affected by the pathogen populations supports the previously mentioned observations that, in the vicinity of tubers, antibiosis and possibly also nitrogen-related process are important in CS disease control (Figure 1, Table 3).
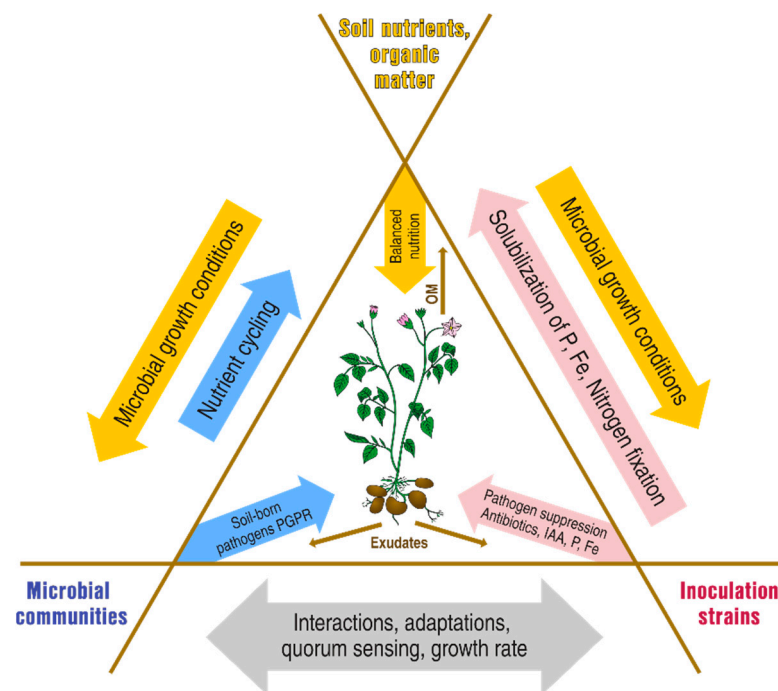
Figure 1. Interactions of soil components, microbial communities, introduced biocontrol strains and potato plants in a system affected by common scab.

The research also demonstrated that the plant–microbe interactions connected to CS severity are detectable only in the nearest vicinity to the potato tuber. In particular, out of the potato tuberosphere, rhizosphere, root zone or bulk soil, the effects of manipulations were detectable only in the tuberosphere soil [23,28]. That closely connects the soil and plant microbiomes, which seem to share not only members but also functions such as activation of both basal and inducible plant defense systems [25,140].

The changes in the microbial community associated with increased CS control might be achieved by addition of specific organic compounds, but also by addition of nutrients (see above).

Consequently, the current knowledge on microbial interactions in the rhizosphere is still limited in terms of being clearly resolved in terms of CS control. However, many examples of successful manipulation of microbial communities by supplementation or cultivars are already available to consider for the improvement of soil health.

5. Inoculation with Antagonistic Strains

Disease occurrence is often accompanied by changes in microbial communities such as altered microbial abundance, composition and function, which are studied as markers of soil health but also for their potential to set conditions favorable for plant protection. Various taxa participate in those activities, or their combinations [22,141].

CS-suppressive soils revealed that non-pathogenic *Streptomyces* act as the agents responsible for suppression [129,130]. However, different studies showed that a broad range of bacterial and fungal taxa contribute to CS suppression, with antagonistic activities found in strains of the genera *Streptomyces* [142–145], *Bacillus* [146,147], *Brevibacillus* [148] and *Pseudomonas* [149], and they were successfully used to control the disease in pot and field trials (Table 4).

Application of the individual strains or strains with organic or inorganic fertilization mostly resulted in significant decreases in CS severity (e.g., [143,144,147,150–155]). In a few studies, the suppression of pathogenic strains or the decrease in genes from the pathogenic island were also determined [149,156]. Surprisingly, in some studies, no effect on the autochthonous microbial community was observed after inoculation [111,139], while in others, proportions of several taxa were altered [146].

Table 4. Soil inoculation affecting CS severity, tuber yield and associated bacterial community.

A. Complex Inocula		
Inoculum	**Effect**	**Reference**
Swine feces with coprophilous actinobacteria	CS suppression; viable counts of *Streptomyces scabies* decreased, antagonistic fluorescent pseudomonads increased	[156]
Broth treatment and inoculation with antagonistic *Bacillus* sp. in pot assay with sterile soil	CS suppression by 40%	[154]
Pseudomonas mosselii with vermicompost	CS suppression	[150]
Bacillus subtilis GB03 and *Rhizoctonia solani* hypovirulent isolate Rhs1A1, compost	CS suppression by 10–34%, increased yield, reduction in stem and stolon canker by 20–38%, black scurf by 30–58%	[151]
Trichoderma virens, Bacillus subtilis and *Rhizoctonia solani*, compost, rapeseed rotation	Reduced disease and increased yield	[92]
Vermiculite cultures of non-pathogenic *Streptomyces* isolates mixed with soil	CS suppression	[157]
Conducive soil inoculated with *Streptomyces* isolates	No effect of inoculation; variability of streptomycete community increasing from planting to mid-season (by pyrosequencing); pathogen suppressive capacity of antagonistic streptomycetes negatively correlating with CS severity (by cultivation)	[111]
B. Individual strains		
Inoculum	**Effect**	**Reference**
Streptomyces melanosporofaciens EF-76 in chitosan beads	Increased numbers of geldanamycin-resistant actinobacteria on harvested potato tubers	[142]
Pesticide and antibiotic-resistant *Streptomyces* spp.	CS suppression by 55–>60%	[144]
S. violaceusniger AC12AB	CS reduction up to 90% in greenhouse and field, increased yield up to 26.8% in field trial	[145]
Streptomyces sp. WoRs-501	CS severity decreased by 78–94% in field pot trial	[143]
Streptomyces strain 272	CS severity reduced by 43% on susceptible potato cultivar Bintje, both disease incidence and severity reduced by 43 and 59% on the scab-tolerant cultivar Nicola	[158]
Pseudomonas fluorescens LBUM223	CS reduced by approximately 30% in plots after biweekly applications, increased yield by 46%; did not reduce pathogen soil populations, down-regulated *txtA* expression in the geocaulosphere	[149,159]
Bacillus megaterium KBA-10, *P. putida* K-19B, *B. megaterium* TV- 91C, *Pantoea agglomerans* RK-92	Biocontrol efficacy 18.7–60.3%, tuber yield increase by 20.4–40%	[160]
B. subtilis and *Trichoderma harzianum* in diatomaceous earth (225–300 kg ha^{-1})	CS index decreased by 30.6–46.1%; 19-23-fold higher *Pseudomonadales*; CS severity negatively correlated with relative abundances of *Agrobacterium*, *Achromobacter* and *Pseudomonas* and positively with *Acidobacteria*, *Actinobacteria*, *Chloroflexi* and *Gemmatimonadetes*	[146]
Brevibacillus laterosporus AMCC100017	CS severity decreased from 2.60 to 0.77, i.e., biocontrol efficacy 70.51%; reduced pathogen, transient impact on the native bacteria community	[148]
Bacillus subtilis	Decrease in common scab severity up to 70%, and 67% in field trials	[147]
B. amyloliquefaciens Ba01	CS reduced from 14.4 ± 2.9% (naturally occurring) to 5.6 ± 1.1% in the field	[161]
B. velezensis 8-4	CS control efficiency reached 51.83 ± 8.53%, the yield increased by 19.91 ± 3.56%	[155]
Trichoderma virens	Decrease in CS incidence and severity	[92]
Phages Stsc1 and Stsc3	Prevented CS symptoms on radish seedlings	[162]

Table 4. *Cont.*

C. Mechanisms of CS suppression		
Biocontrol Strain	**Observed Property**	**Reference**
Streptomyces violaceusniger AC12AB	Production of azalomycin, indole-3-acetic acid and siderophores, nitrogen fixation and phosphate solubilization => CS reduction up to 90% in greenhouse and field trials, increased yield up to 26.8% in field trial	[145]
Pseudomonas fluorescens LBUM223	Phenazine-1-carboxylic acid (PCA) production => growth inhibition of *S. scabiei*, repression of thaxtomin biosynthesis genes (*txtA* and *txtC*); activities were lost in *phzC$^-$* mutant deficient in PCA production	[163]
	Phenazine-1-carboxylic acid production => 12%–14% of all *S. scabiei* genes were differentially expressed, including key genes involved in pathogenicity/virulence, mycelium differentiation and increased oxidative stress	[164]
Fragments of γ-glutamyl transpeptidase from *Bacillus subtilis* BU108	In vitro growth inhibition of *S. scabiei*	[165]
S. melanosporofaciens EF-76	Geldanamycin production => disease index was reduced from 6.30 to 4.81 and from 2.83 to 2.49 in growth chamber and field experiments, respectively	[166]
Streptomyces A1RT	Production of isatropolone C and indole-3-acetic acid => reduction in average disease severity index by 82.4–95.7%	[4]
Streptomyces isolates (strains 93 and 63) and their spontaneous mutants	The mutants lost in vitro inhibitory activity against *S. scabiei* in antibiotic and co-plate assay, while retaining the biocontrol ability in soil	[167]
B. amyloliquefaciens subsp. *plantarum* FZB42	Production of cyclic lipopeptides and volatiles => pathways of induced systemic resistance	[168]
Agrobacterium tumefaciens C58 *attM* gene introduced to *S. scabiei*	No disease symptoms in planta, altered morphological differentiation—quorum quenching paralyzing γ-butyrolactone signaling pathway	[161]

The variation in the microbial community response might be connected to the mechanisms of suppression provided by the inoculated strains. Mostly, production of antibiotics against the pathogens is involved, while the identified compounds include geldanamycin [166], phenazine-1-carboxylic acid [163,164], isatropolone C [4], azalomycin [145] or antimicrobial peptides [154,165]. However, the strains also produce compounds such as indole-3-acetic acid or siderophores and enable nitrogen fixation and phosphate solubilization [145] or remove signaling through γ-butyrolactone pathway [161].

In conclusion, the inoculated strains control CS severity not only directly by antibiosis against pathogens but also through nutrition, metabolism and signaling in the plant–soil–microbe interactions. Thus, it seems that inoculation with locally isolated biocontrol strains may be a safer and more effective approach compared to application of globally distributed products, because the local strains might be more adapted to local soil and climate conditions and also to local microbial communities. That might be useful not only for lower disturbance but also for easier adaptation of inoculated strains [31,169].

6. Conclusions

Soil mineral nutrients are often in an unbalanced state due to fertilization and intensive soil exploitation by agriculture practices [64]. That negatively affects plant growth, productivity and health as well as soil quality and biodiversity. This review suggests that balanced nutrition together with promotion of suppressive microbial communities represent key components in the management of potato common scab. Two approaches can be used to improve the current state of soil, which leads to improved CS suppression. Firstly, supplying soils with the limiting nutrient and/or microbial strain(s) that solubilize the missing nutrients, and secondly, supporting microbial communities that are competitive or antagonistic to the pathogen by addition of peat or a long-decomposed and largely recalcitrant organic matter. In contrast, additions of organic matter or fertilizers containing high amounts of nitrogen should be carefully evaluated, because nitrogen recycling seems to influence CS severity in both directions. To further support CS suppression, it is necessary to carefully select potato cultivars according to their different micronutrient requirements

and accumulation [44,71]. Furthermore, it is important to consider that individual cultivars have various interactions with rhizosphere microorganisms, and those may enhance but also diminish the plant–microbe interactions [28,33,135]. Inoculated biocontrol strains affect not only the pathogen but also the potato plants, the autochthonous microbial community and the soil chemistry, so their impact on the local microbial community also needs to be evaluated prior to their application. Soil chemical status and organic matter should be regularly assessed in more detail to determine the missing elements and the quality of humus.

Focusing on future research, more attention should be paid to plant–microbe–soil interactions occurring in the nearest compartments surrounding potato tubers. These may include the transfer of microorganisms between soil and plant microbiomes, decomposition pathways which lead to compounds influencing the pathogenicity of streptomycetes or metagenomic and metabolomic studies aiming to determine the processes involved in the development of soil suppressiveness. Although long-term monoculture was suggested as the best strategy to achieve long-lasting suppression by streptomycetes [31], new knowledge about the general suppression of CS may bring novel inspiration for management of the disease.

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