*applied microbiology*

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# Reviewing the Current Understanding of Replant Syndrome in Orchards from a Soil Microbiome Perspective

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**Abstract:** Replant syndrome (RS) of fruit and nut trees causes reduced tree vigor and crop productivity in orchard systems due to repeated plantings of closely related tree species. Although RS etiology has not been clearly defined, the causal agents are thought to be a complex of soil microorganisms combined with abiotic factors and susceptible tree genetics. Different soil disinfection techniques alleviate RS symptoms by reducing the loads of the deleterious microbiome; however, the positive effect on crop growth is temporary. The goals of this paper are: (1) to conceptualize the establishment of the syndrome from a microbiome perspective and (2) to propose sustainable solutions to develop a beneficial microbiome to inhibit the onset of RS.

**Keywords:** replant syndrome; replant disease; soil sickness; phytopathogen; beneficial microbes; soil microbiome; orchard management

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**Citation:** Newberger, D.R.; Manter, D.K.; Vivanco, J.M. Reviewing the Current Understanding of Replant Syndrome in Orchards from a Soil Microbiome Perspective. *Appl. Microbiol.* **2023**, *3*, 856–866. https://doi.org/10.3390/applmicrobiol3030059

Academic Editor: Alessandro Vitale

Received: 11 July 2023
Revised: 31 July 2023
Accepted: 1 August 2023
Published: 4 August 2023



## 1. Introduction

The agronomic challenges that arise during the re-establishment of a closely related tree fruit/nut species are collectively known as replant syndrome (RS). RS symptoms can be observed in the first replant generation (second orchard generation) and persist for several years or even decades [1,2]. RS has been vaguely characterized by reduced tree growth, lifespan, fruit yield, and fruit quality attributes such as soluble sugar level and sugar–acid ratio [2–5]. More descriptive characterizations have included reduced branching, shortened internodes, deformed leaves, root necrosis/discoloration, and reduced root growth [4–7]. However, even these more descriptive symptoms are not diagnostic [8] and often trees grown in replant soils need to be compared to trees grown in previously non-orchard soils in order to fully grasp the detrimental consequences of replant syndrome. Furthermore, most reports of RS longevity in the soil are merely anecdotal, since controlled research paired with accurate and detailed, multi-decade cropping histories has been practically impossible to obtain [9,10].

In addition to ambiguous symptom descriptions, there is no consensus on terminology as synonyms for RS include soil sickness, soil fatigue, replant problem, replant disease [11], soil exhaustion, replant disorder [12], and specific replant disease [13]. Here, the term replant syndrome is used since the condition's onset is driven by repeated monocropping [14,15]. Additionally, while a "disease" has distinguishing symptoms typically derived from a single known cause (i.e., a specific pathogen), a "syndrome" refers to a group of signs, phenomena, or symptoms that occur together [16] with an uncertain underlying primary cause.

There is no unanimous agreement on the etiology of RS, which has largely remained an enigma for over 300 years [7,17]. The mechanisms by which consecutive monocultures give rise to a decline in crop productivity are still subject to debate. While RS has been reported in many crops, its negative impacts have been more notable among fruit/nut trees in the

*Rosaceae* family such as almond [18], apple [12], cherry [19], pear [19], and peach [6,11]. Citrus species (*Rutaceae* family) are greatly affected by RS [20,21]. Multiple factors such as autotoxin production leading to accumulation, an imbalance of soil nutrients, and an imbalance of the microbial community structure have been credited with exacerbating RS [20]. While abiotic factors such as autotoxins and nutrient imbalance decrease soil fertility [22], they are not necessarily the direct cause of RS, but rather, may increase the survival and competitiveness of phytopathogens [23]. A critique of the idea that autotoxicity relates to RS is that fallow periods of up to three years fail to suppress RS and improve tree growth [24]. While chemicals causing autotoxicity are unlikely to be stable enough to persist for years, they may result in longer-term shifts in the soil microbiome [23]. Thus, instead of one specific phytopathogen, the primary cause of RS is suspected to consist of a complex of soil phytopathogens which have been shown to be enriched by autotoxins [10,25]. For example, *Panax notoginseng* was found to produce autotoxic ginsenosides which enriched potential phytopathogens (*Alternaria*, *Cylindrocarpon*, *Fusarium*, *Gibberella*, and *Phoma*); meanwhile, relative abundances of beneficial taxa (*Acremonium*, *Mucor*, and *Ochroconis*) decreased [25]. As the microbiome shifts, plant-growth-promoting microbes could become outnumbered by phytopathogens.

Microbiome shifts as the possible underlying cause of RS is further supported by studies showing that plants grown in autoclaved RS soil experience a remarkable increase in growth relative to plants grown in untreated replant soils [11,26,27]. Similarly, fruit tree biomass has been shown to increase in RS soils treated with chemical fumigation, resulting in reduced microbial biomass carbon with no apparent effect on other soil properties (basal respiration, ergosterol content, pH, electrical conductivity, and most nutrient and metal contents) [22]. Finally, when apple trees exhibiting RS symptoms were transplanted from RS soils into healthy soils the RS symptoms reversed [23].

This reversibility is particularly interesting given the identification/involvement of several potential soilborne plant pathogens in RS. For example, phytopathogens frequently associated with RS are oomycetes *Pythium* and *Phytophthora*, bacterial taxa from actinomycetes and genera of *Bacillus* and *Pseudomonas*, and the root lesion nematode [5,22]. Fungal suspects are *Cylindrocarpon*, *Rhizoctonia*, *Fusarium* sp., *Alternaria* sp., *Myrothecium verrucaria*, and *Mycelia sterilia* with many of these taxa being frequently isolated from the rhizosphere (soil surrounding plant roots) [6,23]. However, microbe–microbe and microbe–plant interactions are complex, and site-to-site variation has yielded contradicting results. For instance, *Phytopythium vexans* was found to be a pathogen in one site but acted as a biological control at a different location [6]. Virulence differences of *P. vexans* strains compounded with different abiotic or biotic soil factors could explain these discrepancies [6].

In summary, the diversity and abundance of phytopathogens cause RS, with abiotic factors and autotoxicity instigated by the previous monocrop acting as positive feedback mechanisms for phytopathogen recruitment and development. RS etiology appears to depend not only on the presence of phytopathogens but also on the overall balance of the soil microbial community.

## 2. Developing a Soil Microbiome Model to Understand Replant Syndrome

Tree growth in an orchard's second generation (replanting) is not as vigorous as its first generation. Often, young, transplanted trees die in sites exhibiting severe RS [7]. Additionally, peach seedlings display reduced height and trunk width compared to a control group grown in fumigated soil in as little as 10 weeks [6]. Some studies have found that shoot growth was reduced by 66.9–71% with shoot masses staying consistently low after multiple replanting generations [2]. Less severe cases have noted that trees can overcome an initial delay in growth, eventually reaching the size and annual yields of those grown in healthy soils [28,29]. Nonetheless, recovery is time-consuming, taking valuable years and resources, which ultimately reduces the profitability of the orchard [4]. In these less-severe sites, the fruiting of trees can be delayed 2 to 3 years and still never attain comparable yields to those of the first cycle of planting [7]. Even in instances where RS causes a reduction in fruit yield or a shortened production life without ending in plant death, the resulting reduction in profits has been estimated at 10–20% [6].

RS can persist in fallowed soil for several years or even decades following the removal of the first established orchard [12,24]. It is believed that RS symptoms can be observed even if the roots of previous plants were in an area for only a few months. When young saplings are transplanted, the young root systems interact with populations of phytopathogens from the plant matter residue of the previous trees. There are examples of literature indicating younger plants are more susceptible to diseases compared to their adult counterparts [27]. As such, peach saplings are known to struggle in RS soil.

Traditionally, it is believed that RS primarily affects the next cropping cycle if the consecutive plant species are closely related (i.e., peaches following peaches). Specific RS, like specific apple replant disease, is a buildup of non-generalist pathogens tailored for the genotype of the host tree with host plant residues playing a key role [8]. This would support the possibility that with a decrease in the number of tree hosts, there would be a decrease in the specific replant microbes. Nonetheless, even with the removal of tree hosts, specific phytopathogens can be sequestered in plant residues until complete decomposition. A non-competing concept is that the pathogen build-ups are often composed of ubiquitous generalists [30]. For example, a build-up of phytopathogenic nematodes has been found to be partially responsible for the nonspecific replant symptoms [8]. Once the orchard is newly planted, the RS microbiome will exponentially colonize these recently introduced tree hosts.

Orchard management practices use natural tree physiology to dictate the processes to which the peach tree should direct its energy [31]. Traditional horticultural practices in orchards do not focus on encouraging the tree host to expend its energy in recruiting beneficial microbes for the sake of immune defense. However, recent studies have investigated sustainable techniques like intercropping and how different cover crops influence soil microbial communities in apple orchards [32]. Plants have been found to use between 5–25% of all photosynthetic net fixation of $CO_2$ for root exudation of carboxylates [33], which are critical for attracting plant-growth-promoting rhizobacteria to the plant [34]. Consequently, there is a possibility that the RS microbiome develops instead of a beneficial microbiome tailored to the peach plant, negatively impacting the peach orchard even within the first generation. The disease may not be readily apparent, and the damage observed may be misidentified as part of the aging process. It is generally agreed that the process of RS is initiated by repeated monoculture, and here it is highlighted that RS begins to establish, even in the first generation, if the fruit trees are relatively asymptomatic [35]. Incidentally, significant shifts in the soil microbial community have been detected between non-cultivated, first-year, and second-year apple trees of the first planting [35]. In support of our hypothesis, when second-generation apple trees were planted in steamed disinfected soils where first-generation apple trees had been grown for only three years, the increase in growth was equal to that achieved in non-cultivated soils [35]. In short, the precursor phytopathogenic replant microbes existed in the soil before the orchard was established and, with time, the environment began to evolve virulent traits that were increasingly effective, building an inhospitable environment for the next planting of fruit trees.

Agricultural practices such as pruning initiate a stress response, which stimulates growth to replace the lost biomass [36]. As a result, exposed tissue can become infected [37]. It is known that common pathogens, like the *Cytospora leucostoma*, have great difficulty colonizing trees except through open wounds induced by injuries such as drought injury, winter injury, or pruning [38]. These wounds allow repeated recolonization/co-colonization of multiple strains of phytopathogens which should increase their virulence as observed in other pathogens [39]. Here, it is posited that the replant microbiome virulence levels build up gradually over time, and microbial populations approach higher levels as the first-generation plants are maturing for the first cycle of growth. The chronological age of a plant has been correlated with increased pathogen resistance [40]. Although immune signaling can increase from early developmental stages to reproductive stages, the fitness of a plant's immune system decreases during the reproductive stage as a possible function of host senescence [40]. These findings need to be correlated for fruit trees with a longer lifespan.

Here, the proposed model (Figure 1) is based on broad patterns in an attempt to link tree development through time and the RS microbiome build-up to monitor the development of RS. The purpose of this model is to represent a hypothetical replant situation. Peach, *Prunus persica*, was selected as the example. The first generation of an orchard is defined as an area where peaches have not been grown previously. The timeline starts with the trees planted from seedlings or transplanted saplings (Figure 1a). First-generation orchards do not exhibit replant symptoms [41], since neither allelochemicals nor the replant microbiome are present in the soil in detrimental concentrations [6,42]. Typically, peach trees take 1–3 years to be established in the soil and have the potential to provide a commercial crop during the second year [32]. As the tree roots are established, the tree canopy is trimmed and trained to bear larger branches that can hold a heavy load of fruit [43]. This is a large energy expenditure since the more trimming, the more vigorous epicormic growth occurs [44]. Peak fruit set starts at 4 years of age for what is considered a mature tree [45,46], and peaks at eight years with yields being around 50–150 pounds of fruit per year [47]. After year 8, the fruit set decreases, with year 12 possibly having minimal fruit sets. In orchards, dwarfing rootstocks are used to reduce vegetative vigor by controlling root growth, which in turn can divert sugars to fruit production, especially in young trees [32]. Peach dwarfing rootstocks typically live about 10–15 years in an intensive orchard setting [47].

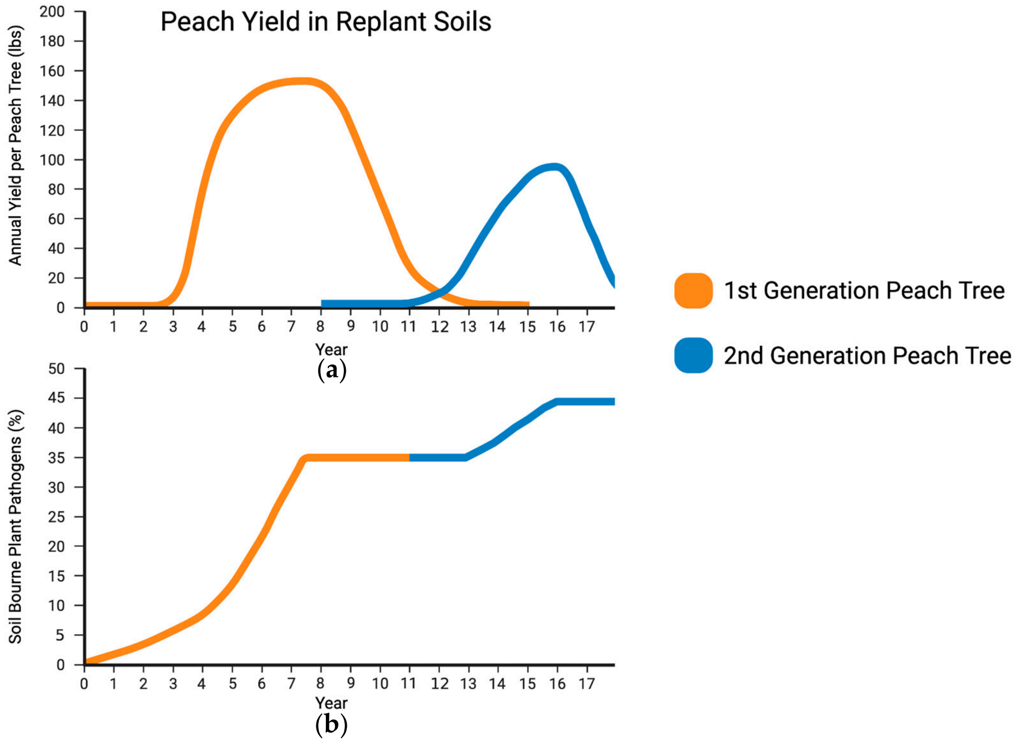


**Figure 1.** Proposed concept of the development of a replant syndrome microbiome. (**a**) First-generation peach trees show expected and typical growth. In the first replanting or second generation, the symptoms of the replant microbiome are observed by the impact it has on the developing fruit tree's crop yield. (**b**) A replant microbiome is established within the first generation of a monocropping orchard. Replant symptoms are immediately evident on newly planted saplings since the pathogens in the soil microbiome have been established previously. Phytopathogens that make up the replant microbiome can potentially specialize to be specific to the orchard genotype, and the pathogenic microbial load is at its peak biomass when crop production is at its highest.

Microbial communities in the bulk soil are extremely diverse, with estimates of 10 billion bacteria classified under thousands of different species in just 1 g of soil [48]. Plants secrete root exudates to culture beneficial microbes in the rhizosphere that are tailored to the plant's needs [49]. However, in addition to symbionts, phytopathogens can also be attracted to this chemical communication (Figure 1b) [50]. Thus, the precursor microbes that make up the RS microbiome are most likely already present in the bulk soil and can proliferate as the composition of the bulk soil shifts [51].

## 3. Breaking the Cycle of Replanting Syndrome

Several solutions have been proposed to combat the problem of RS, each with varying degrees of success. These solutions may be viewed in two ways: (1) a single application of a pre-plant soil disinfection strategy and (2) a continuously implemented biological strategy that increases either plant or microbial diversity. Soil disinfection methods include chemical fumigation, solarization, anaerobic soil disinfestation, autoclaving, soil amendments (*Brassica napus* seed meal, biochar), or even soil replacement in severe cases. Biological strategies are polyculture (cover crops or intercropping), rootstocks, or plant-growth-promoting inoculations and use concepts drawn from the intermediate disturbance hypothesis (IDH). These strategies are designed to avoid the shift towards an RS microbiome.

Pre-plant soil disinfection strategies typically yield more consistent successes, even if temporary, while a biological strategy that increases diversity often varies in success. Sterilization is defined as a process that effectively eradicates all viable microorganisms (including bacterial spores) from a surface or product [52]. Since sterilization of bulk soil is incredibly challenging, the term "soil disinfection" is used here in place of "soil sterilization" to convey a process that reduces the microbial load of a surface [53]. Although other soil microbe eradication techniques such as microwaving and gamma radiation exist, methods such as soil replacement, chemical fumigation, and solarization are the most common practices implemented in orchards for soil disinfection. Pre-plant fumigation has the remarkable ability to reduce RS; however, its benefits are temporary, and it is primarily a pre-plant method. Although chloropicrin has shown effectiveness in reducing RS that was not nematode related, the fumigant was deemed "unpleasant to handle" [54]. Preliminary field and greenhouse trials testing Vorlex have shown promising results and could be an alternative fumigant to chloropicrin for ameliorating RS soils [54]. Currently, chloropicrin is heavily restricted, and Vorlex's registration has been cancelled since 1992. Methyl bromide is a chemical fumigant that was used for RS until 2005 but has since been phased out by U.S. and European governments, since it was found to deplete the ozone layer [55]. Other chemical fumigants, such as Methyl iodide, have been shown to be as effective against RS as methyl bromide [55]. Although methyl iodide does not deplete the ozone layer and was approved by the Environmental Protection Agency in 2008, by 2011 the Pesticide Action Network of North America characterized the fumigant as a neurotoxin and carcinogen [56]. This led Arysta LifeScience to withdraw methyl iodide from the United States and other markets [56]. Chemical fumigants are becoming more restricted since they are considered non-sustainable methods for soil remediation [57]. Solarization, the technique of trapping the sun's radiation in the soil using tarps, has reduced soil fungal phytopathogens such as *Fusaruim* spp., *Verticillium* spp., and *Ilyonectria mors-panacis* (responsible for RS in ginseng) [58]. Anaerobic soil disinfestation builds upon solarization through the addition of carbon substrates and water to the soil, which increases soil temperature and slows down gas exchange [59]. Anaerobic soil disinfestation has demonstrated potential for reducing soil microbial loads (fungi, oomycetes, bacteria, and nematodes) in different soil types and is comparable to soil fumigation [59]. Anaerobic soil disinfestation has been shown to increase trunk cross-sectional area in almond trees by 148–214% compared to controls [59]. Autoclaving the soil as a pre-planting method has increased peach tree biomass [25]. Gamma radiation appears to be the most effective method for soil sterilization [60], but this method is impractical at an orchard scale. In an attempt to reduce RS-related microbes, the complete removal of the RS soils and replacement with healthy/non-pathogenic soil has been in practice [61]. Nonetheless, an inoculation of merely 1% of RS soil is sufficient for the associated microbes to re-establish and reduce tree growth [62]. Soil amendments with *Brassica napus* seed meal were effective starting in the third year of application [24]. Additionally, soil amendments of pinewood biochar (10–20% ($v/v$)) led to an increase in total peach biomass compared to the untreated control [41]. Although effective in reducing RS, these pre-plant soil disinfection strategies are a temporary solution, which provide some relief from RS symptoms.

In terms of the microbiome, how RS develops could follow the intermediate disturbance hypothesis (IDH), which posits that local species diversity is optimized when environmental disturbances are not drastic in terms of magnitude and occur at a regular interval [63]. Although both "magnitude" and "regular interval" are ambiguous [64], the management practices of an orchard—such as irrigation, fertilizer, and pesticides—might provide an ideal environment for pathogens and microbial competitors to enhance their virulence and colonization of the rhizosphere. Since microbes can quickly undergo multiple generations, they can evolve in a relatively short time span. If placed in an ideal setting, bacteria can, therefore, evolve resistance to antibacterial within 10 days [65]. The bulk orchard soil of an orchard experiences much less disturbance than annual crops, so 12 years should be sufficient time for the convergent evolution of several microbes to develop virulent functionalities towards their host.

Biological strategies (cover crops and rootstocks) used to remedy RS are continuously implemented, with success being site-dependent unlike pre-plant soil disinfection strategies [66–68]. These strategies aim to increase diversity in the field by using genetically distinct rootstocks and cover crops, which in turn can increase microbial diversity [40]. Sustainable practices such as increasing plant diversity through polyculture, crop rotation, intercropping, and cover crops have been shown to improve soil health unlike monoculture. Cover crops can improve soil health by increasing nitrogen levels (legumes) or increasing antimicrobial glucosinolates (*Brassica*). Furthermore, the planting of multiple genetically distinct species from the previous crop in polyculture can dilute the build-up of autotoxic compounds by contributing a mix of different plant residues [69]. Although one year of using wheat as a cover crop gave rise to enhanced vegetative growth and apple tree yield, it was not as effective as methyl bromide [24]. A cover crop of wheat showed promising results, but to further reduce RS there needs to be an antimicrobial aspect as well. Incorporation of cover crops which are resistant to generalists phytopathogens, such as nematode-resistant cowpea *Vigna unguiculata* (L.), have been shown to increase tomato yields more than the growth and incorporation of susceptible cowpea or non-incorporation of cowpea [70]. Other promising cover crops that may be used to manage generalist phytopathogens such as plant-parasitic nematodes are *Crotalaria* spp. and *Tagetes* spp. [70–72].

The development of genetic tools such as rootstocks have shown potential. Peach rootstocks with resistance to root-knot nematodes have been developed [73,74]. Furthermore, peach rootstocks—such as Evrica, PAC 9801-02, ROOTPAC® 40, and Tetra—appear to be tolerant to replant soils [75]. Additionally, the drawbacks of monoculture can be mitigated by using rootstocks that are genetically different from their scions which could be used to promote plant diversity while maintaining the same fruit crop type in the orchard [76]. However, RS-resistant rootstocks need to be able to tolerate regional abiotic conditions such as climate, soil type, pH, salinity, etc. [77].

Beneficial microbe inoculums with antimicrobial properties have been developed to enhance crop productivity [78], but these are still in development for RS. Generalized conclusions have surmised that more than 60% of the strains isolated from healthy soils corresponded to *Pseudomonas* sp. [79]. More specifically, *Pseudomonas putida* has been found to isolate suppressed replant-contributing phytopathogens—such as the growth of *Rhizoctonia* and *Pythium* spp. in vitro—and could control *Rhizoctonia* root rot for apple trees [12]. Arbuscular mycorrhiza fungi (AMF) form symbiosis with the roots of approximately 80% of studied land plants [80]. Arbuscular mycorrhiza has been tested by using inoculations of *Acauloapora scrobiculata* in replant soils, resulting in significantly increased shoot biomass and root phosphorus, potassium, calcium, copper, zinc, iron, and boron concentrations [81].

The effect of soil disinfection is effective but temporary and requires a complimentary technique. Figure 2 conceptualizes how the phytopathogen load of peach orchard (orange) soils gradually increase once a tree of the same genotype is re-planted. However, it is possible that, even in untreated soils, the phytopathogen concentrations could plateau. The microbial composition of the rhizosphere, in terms of both bacterial and fungal communities, has been found to be highly variable and to change over seasons and years [4], which could indicate that the players that cause RS shift even within the same site.

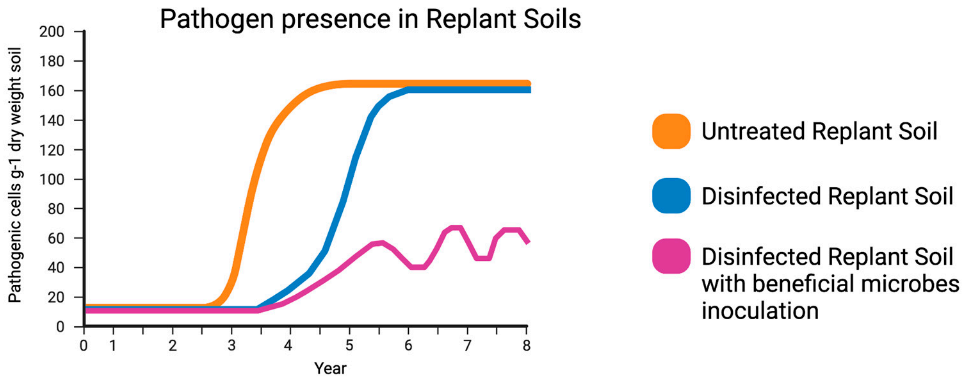


**Figure 2.** Proposed concept of the relative pathogenic gene expression or pathogenic cells g-1 dry weight soil. Phytopathogen load in untreated replant soils of a peach orchard (orange) gradually increases once the host peach tree is planted with possibly plateauing. Phytopathogen load of disinfected replant soils of a peach orchard (blue) show temporary RS relief. Disinfected replant soil with repeated inoculations of beneficial microbes (violet) would fail to remove all phytopathogens but could control RS microbiome populations.

The rhizosphere may not be space-limited, but rather nutrient-limited, since direct observations of roots have shown the majority of the root surface is open space and remains uncolonized [82]. This would mean that the rhizosphere has a carrying capacity, and the total abundance of rhizosphere microorganisms may be consistent with changes occurring in the composition of the rhizosphere [82]. As soil disinfection lowers the phytopathogen population in replant soils of a peach orchard (blue), there is temporary relief from RS. This population could eventually recover, and disinfected replant soils may require continuous measures to increase microbial diversity, such as those highlighted previously.

RS is a multifaceted issue, thus requiring a multifaceted solution. For example, combinations of cover cropping and *Brassica napus* seed meal soil amendment improved the initial peach growth equivalent to a fumigation treatment using 1,3-dichloropropene-chloropicrin [24]. However, using an autoclave as the pre-plant soil disinfection method prior to having the cover crops established, the soil was not amended in a way that was conducive to inducing a biomass increase in the following peach tree planting as compared to the non-autoclaved with no cover crop controls. Additionally, in the same study, not all cover crops induced peach growth equally [26]. Soil disinfection can be challenging to incorporate in multifaceted approaches, since this strategy can decrease not only phytopathogens but beneficial bacteria like nitrogen-fixing *Rhizobium* [83]. A common goal of soil disinfection is to reduce all microbial life, which can be accomplished by heating moist soil to 63 °C for 30 min as it is known to eliminate most pathogenic fungi, bacteria, and viruses [84]. However, solarization practices which induced soil temperatures that did not exceed 41 °C at depths of 30–46 cm still greatly reduced soil population densities of fungal phytopathogens such as *Verticillium dahlia* Kleb., *Pythium ultimum* Trow., *Rhizcotonia solani* Kuehn, and *Thielaviopsis basicola* [85]. Similar solarization studies also found that lethal temperatures for thermal sensitive phytopathogens have been reported to be less than 41 °C (ED90 of *Verticillium dahlia* after 14 h at 37 °C, 50–100% mortality of *Rosellinia necatrix*

Berl. ex Prill after 4 h at 38 °C, mycelium mortality of *Phytophthora cinnamomi* after 1–2 h at 38–40 °C, *Macrophomina phaseolina* and *Pythium aphanidermatum* (strongly declined after 24 h at 40 °C) [83]. *Rhizobium* spp. have an upper-temperature limit range of 37–47 °C with some strains still capable of nodulation at 45 °C [86]. Although solarization heat treatment has been shown to decrease soil abundances of *Rhizobium* spp., these bacteria quickly recovered after the establishment of a legume crop [83]. Therefore, a multifaceted solution including soil disinfection and retaining beneficial microbes may benefit if soil temperatures do not go above 41 °C. Regardless, strategies which mitigate RS are not always as effective when they are combined unless all the factors are considered.

## 4. Conclusions

Arriving at a solution to RS will require experts to reach a consensus on RS-related terminology, develop explicit descriptions for its symptoms, define its etiology, and identify its primary phytopathogens. Consistent terminology would facilitate compiling the literature. Explicit symptom descriptions may aid in detangling compound issues like depleted soil nutrients and autotoxicity, each of which can lead to reduced overall plant biomass in monocultures. The buildup of RS-causing microbes needs to be reduced. The soil disinfection method outlined should also allow the survival of beneficial microbes in the soil instead of aiming for the total elimination of the soil's microbial load. Once the microbial load of RS soils is reduced, then multiple continuous biological methods should be used to keep RS under control. Such methods include RS-resistant rootstocks, poly-cropping, and inoculations of beneficial microbes. Continuous efforts to use these biological methods to increase plant/microbe diversity is critical, since RS-causing microbes will continuously attempt to build up in the soil throughout this time as well.

**Author Contributions:** Conceptualization, D.R.N., D.K.M. and J.M.V., writing—original draft preparation, D.R.N. and J.M.V. writing—review and editing, D.R.N., D.K.M. and J.M.V.; visualization, D.R.N.; supervision, J.M.V.; and funding acquisition, J.M.V. All authors have read and agreed to the published version of the manuscript.

**Funding:** Time dedicated in preparing this review was funded by National Institute of Food and Agriculture/United States Department of Agriculture through a Western Sustainable Agriculture Research Education (SARE), project #SW20-910 with title 'Developing sustainable peach orchard soil microbiome management practices to control replant disease syndrome'.

**Data Availability Statement:** No new data were created in the making of this manuscript.

**Acknowledgments:** The present articles contents are solely the responsibility of the authors and do not necessarily represent the official views of the USDA. Special thanks to Madelene Shehan for reviewing and editing the manuscript for grammar, sentence structure, and syntax.

**Conflicts of Interest:** The authors declare no conflict of interest. The funders had no role in the design of the study; in the collection, analyses, or interpretation of data; in the writing of the manuscript; or in the decision to publish the results.

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