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Root Dynamics of Peach Replant Tolerant and Susceptible Rootstocks in Soils with Different Cropping History

Amaya Atucha*

Department of Horticulture, University of Wisconsin-Madison, 1575 Linden Drive Madison, WI 53706, USA

Abstract

Replant disease (RD) is a major constraint for the establishment of economically viable tree fruit production systems. The use of tolerant rootstocks is considered the most cost-effective and long-term sustainable option to manage RD. The present study examines root production and lifespan of a replant tolerant and susceptible peach rootstock in a replant and non-replant soil. RD susceptible rootstock genotype Lovell and RD tolerant rootstock genotype Viking were established in a replant and non-replant site. Aboveground growth was determined by measuring the tree-trunk cross sectional area annually, and belowground root dynamics were tracked during a 2-year period using minirhizotron technology. Viking trees were significantly larger than Lovell in the replant site only. No significant differences were observed on the number of new roots produced by the two rootstocks in the replant or non-replant sites. In the replant site, roots of Viking remained white for a longer period of time, had higher AMF colonization, and second order roots had longer lifespans than those of Lovell rootstock; however no differences were observed between rootstocks in the non-replant site. Future research on identification of host defense mechanisms is needed for the development of tools that will support and accelerate breeding of resistant rootstocks.

Keywords: Replant disease; Rootstock; Fine roots; Soil borne pathogens

Introduction

Soil borne diseases affecting the fine-root system of plants are a significant limitation for the establishment, survival, and growth of woody perennial trees [1-3]. The severity of these diseases and the manifestation of their symptoms depend on the plants' physiological state, biotic factors, and soil fertility, which in addition to multiple casual organisms [2] significantly challenge their management and control. Replant disease (RD), is characterized by poor growth and high mortality of young trees established in orchards where the same or closely related species were previously planted. Numerous factors have been implicated in RD etiology, including abiotic factors such as soil nutrient depletion, degradation of soil structure, and phytotoxity from allelopathic toxins in plant roots [4,5]. However, the majority of data derived from studies of soil biology in orchards have defined a complex of pathogens as the casual agents of the disease [2]. A core group of soil pathogens has been associated with RD including *Rhizoctonia solani* Kuhn, *Cylindrocarpon* spp., *Pythium*, *Phytophthora*, and pathogenic nematodes [6,7]. Studies of peach replant disease have also identified species of the genera *Trichoderma* and *Fusarium* and *Pratylenchus penetrans* (Cobb) Filip & Schur. Stekh. among the most abundant fungi and parasitic nematodes in peach orchard soils [8,9].

Rootstocks can vary significantly in their performance in replant soils [10,11]. The susceptibility of root tissue to pathogen colonization changes as root tissues mature and as distance from the root tips increases [11,12]. As root tissue matures, suberin barriers at the exodermis and endodermis develop, limiting the uptake of water and nutrients [13], as well as affecting colonization by soil microbes [14]. Additional aspects of secondary development in roots, including the formation of secondary vasculature and woody periderm, and the loss the cortex, may also change the allocation of resources to pathogen defenses [11,15]. Allocation of resources to defense compounds and the susceptibility to pathogen colonization may vary depending on the root hierarchical branching order. If plants allocate defense resources based on the importance of the tissue for plant fitness and the cost of having the tissue removed [16], then higher order roots may have preference for defense resource allocation over lower order roots, because a significant fraction of the root system depends on their function [17,18]. In a study of pathogen abundance and defense compounds at an apple replant site, Emmett et al. [11] found that RD pathogens predominantly colonized first and second order roots and that higher order roots presented greater concentrations of defense compounds. Comparisons between RD susceptible and tolerant apple rootstocks have also reported a link between a greater production of higher order roots and greater RD tolerance [10]. Root system pest tolerance mechanisms based on greater root proliferation and turnover, possibly at the expense of defense allocation have been reported in several woody perennial crops [10,19-21]. Additionally, differences in chemical signaling compounds produced by roots with contrasting growth rates could influence the rate of colonization soil microorganisms [22-24] ultimately affecting the performance of rootstocks under replant conditions [25].

In this study, we examined root dynamics of a RD susceptible and RD tolerant peach rootstock under replant and non-replant soil conditions over a two-year period. We hypothesized that rootstock tolerance to RD is supported by a greater fine root production and faster root turn over, and predict that differences in tree performance between rootstocks will be maintain under replant and non-replant soil.

***Corresponding author:** Amaya Atucha, Department of Horticulture, University of Wisconsin-Madison, 1575 Linden Drive, Madison, WI 53706, USA, Tel: 608-262-6452; E-mail: atucha@wisc.edu

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Materials and Methods

Site and plant material

The study site was located at Colorado State University's Orchard Mesa Research Station in Grand Junction, CO (39°02'28. 9"N 108°27'54. 5"W), and consisted of two separate sites, replant and non-replant, of 0.3 ha each. The replant site had been a peach orchard since 1990; old peach trees had been removed in 2008. The non-replant site had no history of peach production and had been a vineyard block from 1989 to 2003, and converted into an alfalfa field from 2002 to 2008. During summer of 2009 both sites were ripped repeatedly, in a direction parallel to the old tree rows, with a chisel plow to 40 cm depth to help break up layers of compacted soil. Soil in both sites were of similar characteristics (Table 1), a Blackston gravelly loam derived from sandstone and shale in the replant site, and a Gyprockmesa clay loam derived from shale over cobbly alluvium in the non-replant site. Both sites had well drained soil, with more than 1.5 m of depth to a restrictive feature.

During 2011, peach trees were established at 0.9 × 4.8 m spacing. Trees were 'Sierra Rich' peach scion variety on 2 rootstocks: 'Viking' and 'Lovell'. Viking rootstock is an interspecific rootstock originated from the cross Nemaguard rootstock and 14H528 selected seedlings [Prunus amygdalus cv. Jordanolo x Prunus blireiana (Prunus cerasifera cv. 'Atropurpures' × Prunus Mume apricot)]. These new hybrid selections have shown superior performance in replant sites and have shown resistance to root-knot nematodes and tolerance to replant conditions [26,27]. Lovell rootstock is a *P. persica* seedling and the industry standard; it has shown high tree mortality and suppressed growth when established in replant sites [28]. The irrigation system consisted of two lines of drippers for each tree row, with each orifice emitting 4 Lhr^{-1} through two drippers place at 0.25 m on opposite sides of the tree, for a total of 4 drippers per tree. All trees were fertilized each year during the growing season using a 20-20-20 foliar formulation equivalent to 4.5 kg N ha^{-1}, 4.5 kg K ha^{-1}, and 4.5 Kg P ha^{-1}. In addition, a foliar formulation (Albion Multimineral, Albion Minerals UT, USA) was applied twice a year during 2011, 2012, 2013, and 2014 at a rate of 6.8 kg ha^{-1} containing 1% Ca, 1%Mg, 0.5% Cu, 0.5% Fe, 0.5% Mn, 0.1% Mo, and 0.5% Zinc. Glyphosate herbicide was applied annually at a rate of 2.5 kg a.i. ha^{-1} in early May and July to eliminate weeds in a 1.5-m wide strip centered on the tree rows. Insect and disease pest were controlled following standard practices for peach production in Colorado [29]. Tree-trunk cross sectional area (TSCA) was recorded first during tree establishment (2011) and thereafter annually during winter season (January-March) at a permanently marked height (30 cm above ground) to estimate annual and cumulative increases in tree size.

The experimental design consistent of 2 sites: replant and non-replant. The replant site was planted in panels of 4 trees, consisting of 4 different rootstocks planted in the following order: Nemaguard, Lovell, Viking, and Saint Julien. For this study only rootstocks Lovell and Viking were evaluated. The replant site consisted of 5 panels, and in each there were one Viking and one Lovell tree, for a total of 5 trees on Viking rootstock and 5 trees on Lovell rootstock in the replant site. The non-replant site was planted in panels of 10 trees of the same rootstock. There were a total of 10 panels randomly distributed: 5 panels of trees on Viking rootstock and 5 panels of trees on Lovell rootstock, for a total of 50 trees on each rootstock in the non-replant site. Tree growth and total root production data were recorded for 5 trees of Viking and 5 trees of Lovell in each site.

Variable	Replant (n=6)	Non-Replant (n=6)	p-value
Organic Matter (%)	1.95 ± 0.09	2.05 ± 0.15	0.4401
pH	7.97 ± 0.03	7.92 ± 0.01	0.4560
P (ppm)	5.01 ± 0.02	5.33 ± 0.21	0.1747
K (ppm)	163.00 ± 17.58	164.17 ± 22.56	0.9798
Mg (ppm)	405.33 ± 18.02	412.33 ± 10.91	0.7122
Ca (ppm)	4707.3 ± 68.93	5044.67 ± 157.9	0.1621
CEC ($cmol \cdot kg^{-1}$)	28.33 ± 0.61	30.50 ± 0.72	0.1422

Table 1: Soil nutrient, pH, and organic matter content for non-replant and replant research sites collected in 2017.

Minirhizotron tube installation and image observation

Root populations were observed through transparent polycarbonate minirhizotron (MR) observation tubes, 0.5 m long and 0.05 m outer diameter. Two tubes per tree were installed during summer of 2012 at 45° from the vertical on either side of the tree, parallel to the tree row, and at 0.4 m from the tree trunk. A total of 40 tubes (20 in the replant and 20 in the non-replant sites) were installed in the entire study. In the replant site, 5 out of the 30 panels were selected, and tubes were installed in the Lovell and Viking rootstock (2 tubes per tree, 5 panels, 2 rootstocks). In the non-replant site tubes were installed in all 10 panels, with one tree per panel for Lovell and Viking rootstock (2 tubes per tree, 10 panels, 1 tree per rootstock).

To allow time for root growth, no images were recorded until the following year. Root images were then recorded biweekly with a MR digital video camera Model BTC-ICAP (Bartz Technical Co, Santa Barbara, CA, USA). Root images were recorded biweekly starting 15 March to 25 October in 2013, and from 28 March to 15 October in 2014 and 2014. A total of 32 sessions recorded during the study.

Root observation and measurements

Date of individual root appearance, disappearance, root order, as defined by Fitter [30], and date of pigmentation or browning (date root was seen as a color other than white) were recorded with WinRhizoTron MF (Regents Inc., Quebec, Canada). Roots were considered dead when they became black and shriveled [31] or if the root disappeared from a viewing location and did not reappear. Root diameter was measured at the time of root birth. A total of 3,667 roots were tracked and used for analysis, among those roots 49% were right-censored (i.e. still alive at the final observation).

AMF colonization

Root samples were collected during July of 2013, using a stainless steel core of 7 cm internal diameter and 15 cm depth. Two soil core samples were collected from all of the trees with minirhizotron observational tubes (5 Viking and 5 Lovell trees in the replant site and 5 Viking and 5 Lovell trees in the non-replant site) at 0.2 m distance from the tree trunk, at opposite sites of the tree trunk. Soil cores were washed over a 500 μm sieve, and roots from both cores of a single tree were pooled as a single experimental unit. Fine roots, defined as first and second order roots with an intact cortex, were selected and stored in FAA (formaldehyde: acetic acid: alcohol 5%:10%:50% v/v) solution for one month before clearing and staining. Roots were cleared and stained following the protocol by Comas et al. [32]. Stained roots were mounted parallel to the long axis of a 7.5 × 5 cm microscope slides with a cover slip. A total of 4 slides were analyzed for each tree. External and internal fungal structures were observed at a 400 × magnification by assessing intersections between root fragments and the eyepiece micrometer at 5-mm intersection intervals. Each point of intersection between the root and micrometer was scored as either (1): mycorrhizal structure (e.g., arbuscules, vesicles, mycorrhizal hyphae, hyphal coils) or (2) non-mycorrhizal structure (e.g., septate hyphae, oospore, zoospores). A minimum of 100 root intersections was examined for a given sample.

Data analysis

Tree growth between rootstocks was analyzed as the absolute difference in trunk diameter between the planting date and the last year of data collection (2011 and 2014, respectively), and analyzed separately for the replant and non-replant site using a pooled t-test due to the small sample size. Soil nutrient content, total root production and root production per root order, was analyzed using ANOVA and data was log-transformed to satisfy the model assumptions. Root diameter and root AM colonization were analyzed using a mixed effect model with tree as a random effect. When significant effects were indicated, means were compared using Student's *t*-test at P<0.05. Kaplan-Meier survival model [33] was used to calculate root lifespan, time to brown, and survivorship estimates. To test the effect of rootstock and soil condition (replant and non-replant) on root lifespan, data were analyzed using the Cox proportional hazards regression [34]. Proportional hazard assumptions were satisfied based on Schoenfeld residuals. A hazard represents the probability of a root dying at a particular given point in time, assuming that the root has survived to that particular point of time [35]. A hazard ratio is then the ratio of hazards between two levels of a covariate (e.g., replant soil *vs.* non-replant soil, tolerant rootstock *vs.* susceptible rootstock) and compares the instantaneous risk of death between the two levels throughout the study period. All statistical analysis was performed using JMP, Version Pro 11 (SAS Institute Inc., Cary, N.C., U.S.)

Results

Tree growth

Peach trees on Viking rootstock grew significantly more than those on Lovell rootstock in the replant site, however there was no difference between rootstocks in the non-replant site (*P*=0.033 and *P*=0.729, respectively) (Figure 1A-B). Four years after planting, Viking and Lovell trees were 56 and 73% smaller in the replant site compared to those grown in the non-replant site.

Root production

There were no significant differences in the number of new roots per tree between rootstocks, either at the replant or the non-replant site (*P*=0.5492 and *P*=0.9756, respectively) (Figure 2). No significant differences were observed between rootstocks in the number of new first or second order roots in either replant or non-replant sites (data not shown).

Root diameter and time to pigmentation

Root diameter was analyzed separately for first and second order roots, as defined by Fitter [30]. There were no significant differences between rootstocks in either the replant or the non-replant site for first or second order root diameters (Table 2). However, first order roots of Viking rootstock were significantly smaller in diameter in the replant site compared to the non-replant site (Table 2).

In the replant site, roots of Viking rootstock remained white for a significantly longer period of time than roots of Lovell rootstock (*P*=0.007, Figure 3), and the risk of becoming brown was 74% that of Lovell roots (Table 3). However, in the non-replant site there were no differences between rootstocks in the risk of roots becoming brown (*P*=0.534). When comparing between replant and non-replant sites, the risk of roots becoming brown in the non-replant site was 70% that of roots in the replant site (*P*<0.0001).

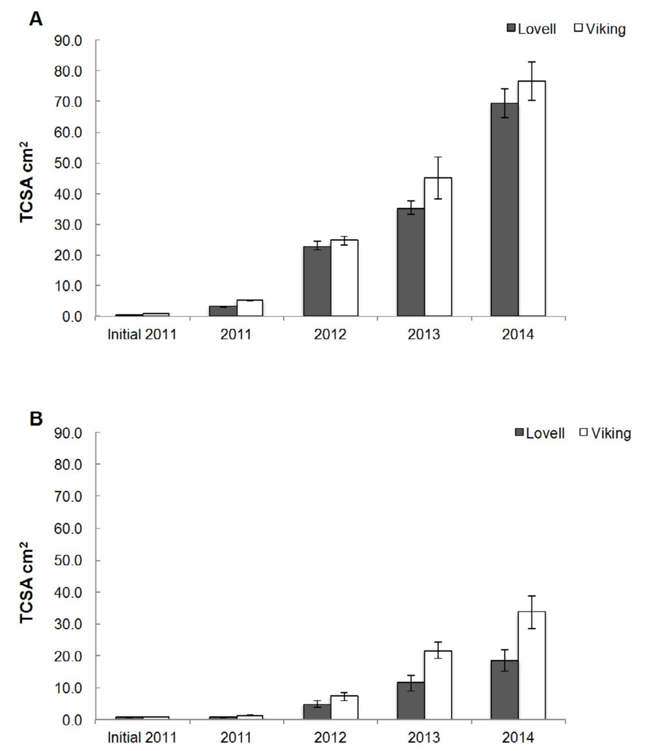

Figure 1: A-B) Trunk cross sectional area (TCSA) of peach trees growing on Lovell and Viking rootstock in a non-replant site (A) and a replant site (B) during first 4 years after tree establishment. Tree growth, analyzed as the difference in TCSA at planting (initial 2011) and the last year of data collection (2014), was significantly higher for Viking rootstock in the replant site compared to Lovell (P=0.033), no differences were observed in the non-replant site (P=0.729). Error bars show s.e. of mean for *n*=5 in the replant site and *n*=5 in the non-replant site.

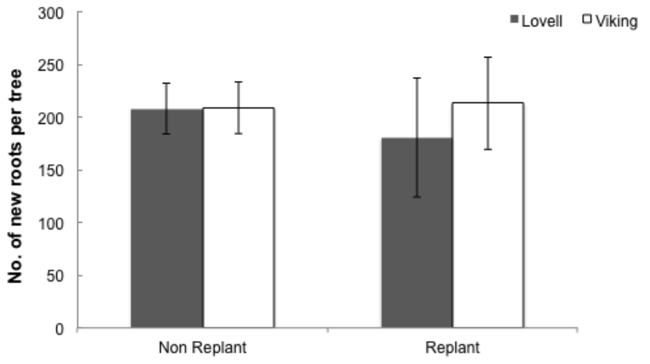

Figure 2: Number of new roots per tree for Lovell and Viking peach rootstock under replant and non-replant soil (*P*=0.9313 and *P*=0.5401, respectively). Bars represent total number of new roots per tree over two-years observation period. Error bars show s.e. of mean for *n*=5.

Roots survival and root lifespan

Regardless of the rootstock, roots in the non-replant site had a survival probability significantly higher than those in the replant site

Root order	Rootstock	Treatment		
		Replant	Non-replant	p-value
1st	Viking (n=968; 754)	0.233 ± 0.006	0.251 ± 0.008	0.0209*
	Lovell (n=668; 948)	0.229 ± 0.028	0.272 ± 0.028	0.1965
	p-value	0.7268	0.325	
2nd	Viking (n=177; 81)	0.455 ± 0.043	0.441 ± 0.048	0.8165
	Lovell (n=144; 91)	0.498 ± 0.029	0. 487 ± 0.079	0.7833
	p-value	0.5662	0.4154	

Values presented are mean and standard error of the mean. Data was analyzed using a mixed effect model, with tree as a random effect; P-values represent mean comparison using Student's t-test for comparison between rootstocks (bottom of the table) and between treatments (right side column).

Table 2: Root diameter (mm) by root order under replant and non-replant soil for Viking and Lovell rootstocks.

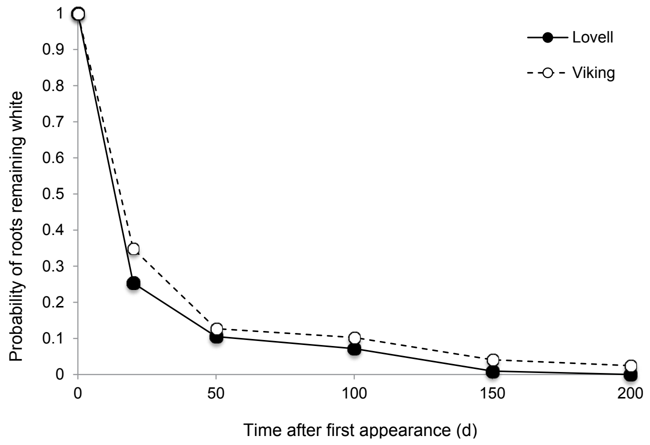

Figure 3: Root probability of remaining white for peach rootstock Lovell (*black circles; n=723*) and Viking (*white circles; n=1,062*) in the replant site. The probability of Viking remaining white was significantly higher than that of Lovell (*P*=0.007).

Variable	df	Parameter estimate	SE	Wald Chi-square	P> chi-square	Risk ratio
Lovell	1	0.149	0.047	9.973	0.001	0.74

Table 3: Results of Cox proportional hazard regression analysis with dependent variable: time to browning under replant soil.

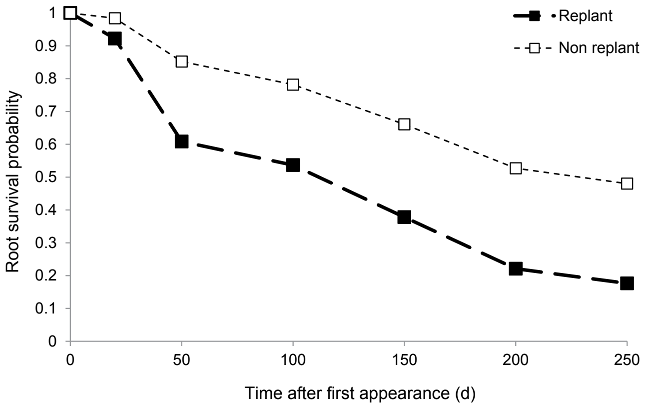

Figure 4: Root survival probability for fine roots in the replant site (*black squares; n=1,232*) and non-replant site (*white squares; n=605*). Roots survival probability was significantly higher for roots in the non-replant site (*P*<0.0001).

(P<0.0001; Figure 4), with a median root lifespan of 211 and 126 days, respectively. When root lifespan was compared between rootstocks in non-replant and replant sites, there were no significant differences (*P*=0.3731 and *P*=0.078, respectively). However, when data was separated by root order, second order roots of Viking rootstocks lived significantly longer than those of Lovell in the replant site (P=0.022, Figure 5A), but no differences were observed in the non-replant site (*P*=0.503, Figure 5B). No differences were observed for 1st order roots between rootstocks in the non-replant or replant site (*P*= 0.964 and *P*=0.264, respectively). Proportional hazard regression analysis using rootstocks as a covariant indicated than in replant soils the mortality risk of Viking second order roots is 64% that of Lovell second order roots (Table 4).

AM colonization

There were no significant differences in the percentage of fine root length colonized by AM between rootstocks in the non-replant site (P=0.692). However, fine roots of Viking showed a significantly higher AM colonization than those of Lovell in the replant site (P<0.001, Figure 6). No significant differences were observed between rootstocks in the percentage of root length containing non-mycorrhizal structures (P=0.838, data non-shown).

Discussion

The nature of rootstock tolerance to RD is not well understood, due in part to its complex etiology, multiple casual organisms, the difficulty of working with root systems, and the lack of standard phenotyping methodology to characterize root resistance to RD pathogens [36]. RD tolerance can vary wildly among rootstock genotypes, as single or multiple mechanisms can be involved in restricting pathogen colonization and disease severity. Recent studies have described several plant defensive mechanisms to RD: selection of beneficial bacterial and fungal communities in the rhizophere [37,38] fast regeneration of fine root systems [10]; and increased defense compound production [11]. Because none of these mechanisms confer resistance, tolerant rootstocks still exhibit decreased growth when established in replant soil compared to fumigated or non-replant sites. In our study, RD tolerant rootstock Viking showed improved performance in the replant site compared to the susceptible rootstock Lovell (Figure 1B). Reports on field performance of highly vigorous plum based rootstocks, such as Viking, have shown lower tree mortality than the peach based rootstocks [27], possibly due to nematode resistance genes [39]. However, four years after planted trees of RD tolerant rootstock Viking exhibited a 53% reduction in trunk growth in the replant site compared to the non-replant site. Identifying plant defense mechanisms against soil borne pathogens is imperative for developing RD resistant rootstocks that can incorporate different defensive strategies and thus lead to greater degrees of tolerance.

High root proliferation and fast turnover has been shown to be an effective tolerance mechanism against soilborne diseases [10,40,41]. Diseased roots are readily shed and replaced by new roots as a strategy to limit pathogen proliferation. Under this scenario, the cost of

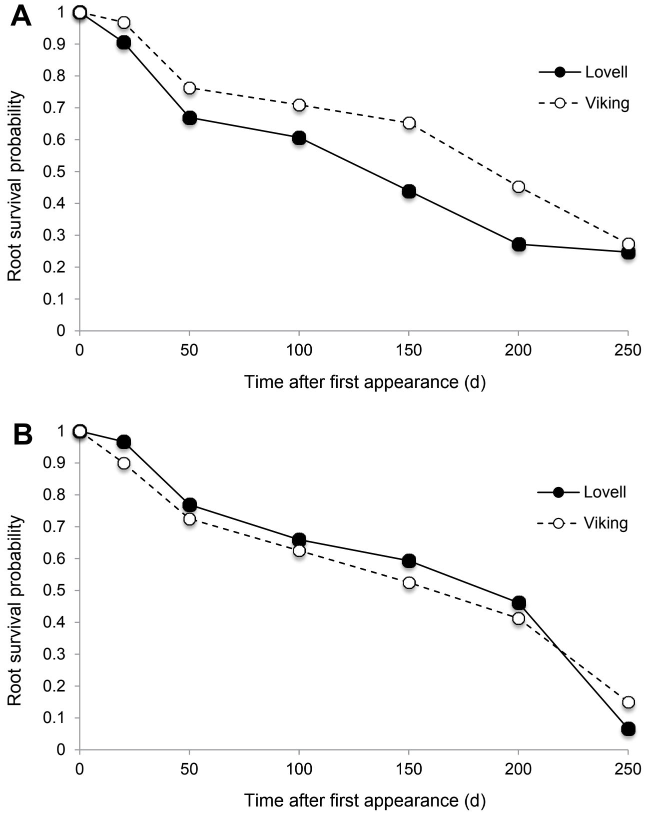

Figure 5: A-B) Root survival probability for 2nd order roots of Viking rootstock (*white circles*) and Lovell rootstock (*black circles*) under non-replant (**A**) (P=0.002) and replant (**B**) site (P=0.503).

Variable	df	Parameter estimate	SE	Wald Chi-square	P> chi-square	Risk ratio
Lovell	1	0.225	0.109	4.151	0.0416	0.64

Table 4: Results of Cox proportional hazard regression analysis for second order roots in the replant soil with dependent variable: root lifespan under replant soil.

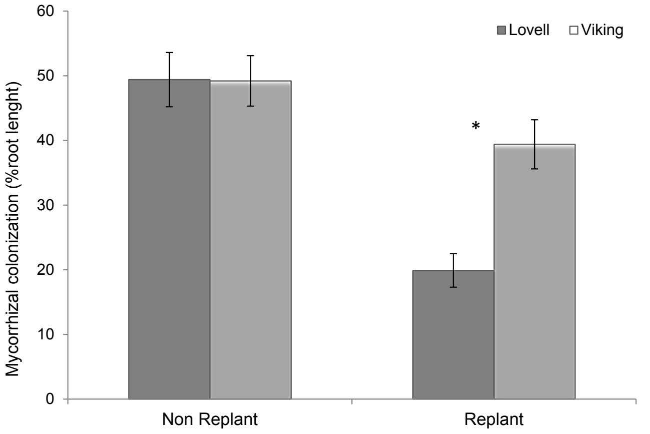

Figure 6: Proportion of fine root length colonized by AM fungi in Lovell and Viking rootstock in a non-replant and replant site. Asterisk (*) denotes significance at P<0.05. Error bars show s.e. of mean for n=20.

sustaining a high production of new roots would be offset by the higher efficiency of new roots in absorbing nutrients and water, as well as the lower carbon investment in these "disposable" roots. We did not detect significant differences in fine root production or root diameter between susceptible rootstock Lovell and tolerant rootstock Viking (Figure 2 and Table 2), although Viking rootstocks had thinner first order roots and both rootstocks presented roots with shorter lifespans in the replant site (Table 2 and Figure 4). Differences in root proliferation between RD-tolerant Viking and RD-susceptible Lovell did not appear to explain the better performance of Viking in the replant site.

Pathogen abundance can vary significantly across root orders [42], with lower order roots having higher concentrations of soil pathogens linked to replant diseases [11]. Lower susceptibility of higher order roots to pathogen colonization is due in part to anatomical shifts, such as loss of cortical tissue and development of secondary vasculature system, which restricts pathogen colonization to specific host tissues. However, rootstock genotypes might differ in anatomical features of roots from the same order. For example, Eissenstat and Achor [43] found that second order roots of citrus seedlings developed secondary xylem and periderm, limiting pathogenic fungal infection of the inner cortex, while second order roots of citrus rootstock cultivars did not undergo secondary development. Although in our study we did not evaluate root anatomical differences between rootstocks, it is possible that differences in rootstock performance in the replant site are linked to secondary development of tissues in lower order roots, which would limit pathogen colonization and thus extend root lifespan as we observed in second order roots of Viking (Figure 5A and Table 4).

Tree root browning (or pigmentation) is linked to significant changes in root anatomical structures [18,44] and physiological function [31,45,46], and can be elicited by external factors such as soil moisture, temperature, fertility, and pathogens or herbivory [10,47-49]. Studies comparing white and brown roots have reported lower respiration rates and reduced metabolic activity of brown versus white roots [31,45], suggesting a decline in nutrient and water absorption capacity following pigmentation [50,51]. Browning of infested roots in several host-pathogen interactions has been associated with increased accumulation of phenolic compounds in affected tissues [51,52]. These phenolic compounds are considered to be involved in plant defense responses [53] such as the hypersensitive reaction in which host cells undergo programmed cell death to block pathogen advance. However, root browning and phenolic compound accumulation in infested roots has also been associated with root necrosis [54,55]. In our study, the significantly higher risk of fine roots becoming brown in the replant site compared to the non-replant site could be the result of damage to the epidermal and cortical tissue of root tips colonized by replant pathogens, which has previously been reported in other replant studies [10,56]. Rootstock differences in rates of browning in the replant site (Figure 3), could be associated with lower population of pathogens in roots of tolerant rootstocks, as reported in previous studies in apple replant disease [11,57,58].

Disease reduction in host plants colonized by AMF is the outcome of complex interactions between plant, pathogen, and AMF. Mechanisms involved in disease suppression by AMF have been mostly attributed to reduction of the pathogen's parasitic growth as a result of the stimulation of host-plant defense reactions and competition for colonization sites [59,60]. Studies comparing different genotypes of chickpeas plants reported that differences in AMF colonization among genotypes was linked to differences in root exudate composition [23,61], suggesting that these plant phytochemicals would be involved in host preference of AMF. Differences in root exudation have been reported for genotypes that differ in their level of tolerance to soil borne pathogens [61], indicating that root exudates can modify soil microbial community to the plant's advantage.

In our study, there were significant differences in AMF colonization between RD tolerant Viking and susceptible Lovell in the replant site only (Figure 6). Lovell and Viking trees were planted next to each other in all replant panels, so differences in AMF colonization were unlikely to be caused by higher soil inoculum pressure in certain areas of the site. We hypothesize that preferential AMF colonization in Viking roots could be linked to differences in the composition of root exudates between rootstocks genotypes. Several studies have reported on the role of root exudates on shaping rhizosphere microbial community structure [62,63], and their possible effect on selecting and promoting beneficial microbial populations in the rhizosphere of RD tolerant rootstocks [25,37].

Conclusion

The use of tolerant/resistant rootstocks is a cost-effective and environment-friendly option to manage soil borne diseases in tree fruit production systems, yet rootstock tolerance mechanisms to soil borne pathogens are not fully understood. Contrary to previous studies comparing susceptible and tolerant RD rootstocks, we did not observe differences in fine root production between rootstocks. However, in the replant site fine roots of tolerant rootstock Viking had longer lifespans, reduce risk of becoming brown and higher AMF colonization than those of susceptible rootstock Lovell. Identification of tolerance and resistance mechanisms to RD pathogens is critical to support breeding efforts for resistant rootstocks, which ultimately offers the most efficient and sustainable option to manage the disease.

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References

1. Gómez-Aparicio L, Ibánez B, Serrano MS, De Vita P, Avila JM, et al. (2012) Spatial patterns of soil pathogens in declining Mediterranean forests: implications for tree species regeneration. New Phytologist 194: 1014-1024.
2. Mazzola M, Manici LM (2012) Apple replant disease: role of microbial ecology in cause and control. Annual Review of Phytopathology 50: 45-65.
3. Packer A, Clay K (2000) Soil pathogens and spatial patterns of seedling mortality in a temperate tree. Nature 404: 278-281.
4. Hofmann A, Wittenmayer L, Arnold G, Schicber A, Merbach W (2009) Root exudation of phloridzin by apple seedlings (Malus x domestica Borkh.) with symptoms of apple replant disease. J Appl Bot Food Qual-Angew Bot 82: 193-198.
5. Zhang JH, Mao ZQ, Wang LQ, Shu HR (2007) Bioassay and identification of root exudates of three fruit tree species. J Integrative Plant Bio 49: 257-261.
6. Mazzola M (1998) Elucidation of the microbial complex having a causal role in the development of apple replant disease in Washington. Phytopathology 88: 930-938.
7. Tewoldemedhin YT, Mazzola M, Labuschagne I, McLeod A (2011) A multi-phasic approach reveals that apple replant disease is caused by multiple biological agents, with some agents acting synergistically. Soil Biology & Biochemistry 43: 1917-1927.
8. Yang JI, Ruegger PM, McKenry MV, Becker JO, Borneman J (2012) Correlations between root-associated microorganisms and peach replant disease symptoms in a California soil. PLoS ONE 7: e46420-e46420.
9. Mountain WB, Patrick ZA (1959) The Peach Replant Problem in Ontario: VII. The Pathogenicity of Pratylenchus penetrans (Cobb, 1917) Filip. & Stek. 1941. Canadian Journal of Botany 37: 459-470.
10. Atucha A, Emmett B, Bauerle T (2014) Growth rate of fine root systems influences rootstock tolerance to replant disease. Plant and Soil 376: 337-346.
11. Emmett B, Nelson EB, Kessler A, Bauerle TL (2014) Fine-root system development and susceptibility to pathogen colonization. Planta 239: 325-340.
12. Watt M, Silk WK, Passioura JB (2006) Rates of root and organism growth, soil conditions, and temporal and spatial development of the rhizosphere. Annals of Botany 97: 839-855.
13. Baxter I, Hosmani PS, Rus A, Lahner B, Borevitz JO (2009) Root Suberin Forms an Extracellular Barrier That Affects Water Relations and Mineral Nutrition in Arabidopsis. PLoS Genet 5: e1000492.
14. Ma F, Peterson CA (2003) Current insights into the development, structure, and chemistry of the endodermis and exodermis of roots. Canadian J Botany 81: 405-421.
15. Guo DL, Mitchell RJ, Hendricks JJ (2004) Fine root branch orders respond differentially to carbon source-sink manipulations in a longleaf pine forest. Oecologia 140: 450-457.
16. McCall AC, Fordyce JA (2010) Can optimal defence theory be used to predict the distribution of plant chemical defences? J Ecology 98: 985-992.
17. Adams TS, Eissenstat DM (2015) On the controls of root lifespan: assessing the role of soluble phenolics. Plant and Soil 392: 301-308.
18. Wells CE, Eissenstat DM (2002) Beyond the roots of young seedlings: the influence of age and order on fine root physiology. J Plant Growth Regulation 21: 324-334.
19. Graham JH (1990) Evaluation of tolerance of citrus rootstocks to Phytophthora root rot in chlamydospore-infested soil. Plant Disease 74: 743-746.
20. Valenzuela-Estrada LR, Bryla DR, Hoashi-Erhardt WK, Moore PP, Forge TA (2012) Root Traits Associated with Phytophthora Root Rot Resistance in Red Raspberry. Acta Hort (ISHS) 946: 283-287.
21. Bauerle TL, Eissenstat DM, Granett J, Gardner DM, Smart DR (2007) Consequences of insect herbivory on grape fine root systems with different growth rates. Plant, Cell and Environment 30: 786-795.
22. Pinior A, Wyss U, Piché Y, Vierheilig H (1999) Plants colonized by AM fungi regulates further root colonization by AM fungi through altered root exudation. Canadian J Botany 77: 891-897.
23. Ellouze W, Hamel C, Cruz AF, Ishii T, Gan Y, et al. (2012) Phytochemicals and spore germination: At the root of AMF host preference? Applied Soil Ecology 60: 98-104.
24. Gianinazzi-Pearson V, Séjalon-Delmas N, Genre A, Jeandroz S, Bonfante P (2007) Plants and arbuscular mycorrhizal fungi: cues and communication in the early steps of symbiotic interactions. Advances in Botanical Research 46: 181-219.
25. St. Laurent A, Merwin I, Fazio G, Thies J, Brown M (2010) Rootstock genotype succession influences apple replant disease and root-zone microbial community composition in an orchard soil. Plant and Soil 337: 259-272.
26. Mestre L, Reig G, Betrán JA, Pinochet J, Moreno MÁ (2015) Influence of peach–almond hybrids and plum-based rootstocks on mineral nutrition and yield characteristics of ‘Big Top’ nectarine in replant and heavy-calcareous soil conditions. Scientia Horticulturae 192: 475-481.
27. Jiménez S, Pinochet J, Romero J, Gogorcena Y, Moreno MÁ, et al. (2011) Performance of peach and plum based rootstocks of different vigour on a late peach cultivar in replant and calcareous conditions. Scientia Horticulturae 129: 58-63.
28. Parker ML, Ritchie D, Nyczepir A (1997) Peach Rootstock Performance of BY-520-9 and Lovell in a Peach Tree Short Life Replant Site. Hort Science 32: 497.
29. Murray M, Larsen H, McCammon T (2015) Intermountain Tree Fruit Production. Utah State University, Logan, UT.
30. Fitter AH (1982) Morphometric analysis of root systems - application of the technique and influence of soil fertility on root-system development in two herbaceous species. Plant Cell Environ 5: 313-322.
31. Comas LH, Eissenstat DM, Lakso AN (2000) Assessing root death and root system dynamics in a study of grape canopy pruning. New Phytologist 147: 171-178.
32. Comas LH, Patterson A, Carlisie B (2011) Arbuscular mycorrhizal (AM) staining and quantification. Prometheus Wiki.
33. Kaplan EL, Meier P (1958) Nonparametric Estimation from Incomplete Observations. Journal of the American Statistical Association 53: 457-481.
34. Cox DR (1972) Regression Models and Life-Tables. Journal of the Royal Statistical Society. Series B (Methodological) 34: 187-220.

35. Allison PD (2010) Survival analysis using SAS: a practical guide. SAS Institute, Cary, NC.

36. Zhu Y, Fazio G, Mazzola M (2014) Elucidating the molecular responses of apple rootstock resistant to ARD pathogens: challenges and opportunities for development of genomics-assisted breeding tools. Horticulture research 1: 14043.

37. Rumberger A, Merwin IA, Thies JE (2007) Microbial community development in the rhizosphere of apple trees at a replant disease site. Soil Biology & Biochemistry 39: 1645-1654.

38. Rumberger A, Yao SR, Merwin IA, Nelson EB, Thies JE (2004) Rootstock genotype and orchard replant position rather than soil fumigation or compost amendment determine tree growth and rhizosphere bacterial community composition in an apple replant soil. Plant and Soil 264: 247-260.

39. Dirlewanger E, Cosson P, Howad W, Capdeville G, Bosselut N, et al. (2004) Microsatellite genetic linkage maps of myrobalan plum and an almond-peach hybrid—location of root-knot nematode resistance genes. Theoretical and Applied Genetics 109: 827-838.

40. Graham JH (1995) Root regeneration and tolerance of citrus rootstocks to root-rot caused by Phytophthora nicotianae. Phytopathology 85: 111-117.

41. Yao SR, Merwin IA, Brown MG (2006) Root dynamics of apple rootstocks in a replanted orchard. HortScience 41: 1149-1155.

42. English JT, Mitchell DJ (1988) Relationships between the development of root systems of tobacco and infection by Phytophthora parasitica var. nicotianae. Phytopathology 78: 1478-1483.

43. Eissenstat DM, Achor DS (1999) Anatomical characteristics of roots of citrus rootstocks that vary in specific root length. New Phytologist 141: 309-321.

44. Gu J, Wei X, Wang J, Dong X, Wang Z (2015) Marked differences in standing biomass, length density, anatomy and physiological activity between white and brown roots in Fraxinus mandshurica Rupr. plantation. Plant and Soil 392: 267-277.

45. Baldi E, Wells CE, Marangoni B (2010b) Nitrogen absorption and respiration in white and brown peach roots. J Plant Nutrition 33: 461-469.

46. Rewald B, Rechenmacher A, Godbold DL (2014) It’s Complicated: Intraroot System Variability of Respiration and Morphological Traits in Four Deciduous Tree Species. Plant Physiology 166: 736-745.

47. Bartsch N (1987) Responses of root systems of young Pinus sylvestris and Picea abies plants to water deficits and soil acidity. Canadian J Forest Research 17: 805-812.

48. Anderson LJ, Comas LH, Lakso AN, Eissenstat DM (2003) Multiple risk factors in root survivorship: a 4-year study in Concord grape. New Phytologist 158: 489-501.

49. Baldi E, Toselli M, Eissenstat DM, Marangoni B (2010a) Organic fertilization leads to increased peach root production and lifespan. Tree Physiology 30: 1373-1382.

50. Volder A, Smart DR, Bloom AJ, Eissenstat DM (2005) Rapid decline in nitrate uptake and respiration with age in fine lateral roots of grape: implications for root efficiency and competitive effectiveness. New Phytologist 165: 493-502.

51. Modafar CEl, Tantaoui A, Boustani EE (2000) Changes in Cell Wall-bound Phenolic Compounds and Lignin in Roots of Date Palm Cultivars Differing in Susceptibility to Fusarium oxysporum f. sp. albedinis. Journal of Phytopathology 148: 405-411.

52. De Ascensao ARDCF, Dubery IA (2000) Panama Disease: Cell Wall Reinforcement in Banana Roots in Response to Elicitors from Fusarium oxysporum f. sp. cubense Race Four. Phytopathology 90: 1173-1180.

53. Mayer AM, Staples RC, Gil-ad NL (2001) Mechanisms of survival of necrotrophic fungal plant pathogens in hosts expressing the hypersensitive response. Phytochemistry 58: 33-41.

54. Owen-Going T, Beninger C, Sutton J, Hall J (2008) Accumulation of phenolic compounds in plants and nutrient solution of hydroponically grown peppers inoculated with Pythium aphanidermatum. Canadian Journal of Plant Pathology 30: 214-225.

55. Sutton JC, Sopher CR, Owen-Going TN, Liu W, Grodzinski B, et al. (2006) Etiology and epidemiology of Pythium root rot in hydroponic crops: current knowledge and perspectives. Summa Phytopathologica 32: 307-321.

56. Caruso FL, Neubauer BF, Begin MD (1989) A histological study of apple roots affected by replant disease. Canadian J Botany 67: 742-749.

57. Isutsa DK, Merwin IA (2000) Malus germplasm varies in resistance or tolerance to apple replant disease in a mixture of New York orchard soils. Hort Science 35: 262-268.

58. Mazzola M, Brown J, Zhao XW, Izzo AD, Fazio G (2009) Interaction of brassicaceous seed meal and apple rootstock on recovery of Pythium spp. and Pratylenchus penetrans from roots grown in replant soils. Plant Disease 93: 51-57.

59. Cordier C, Gianinazzi S, Gianinazzi-Pearson V (1996) Colonisation patterns of root tissues by Phytophthora nicotianae var. parasitica related to reduced disease in mycorrhizal tomato. Plant and Soil 185: 223-232.

60. Pozo MJ, Cordier C, Dumas-Gaudot E, Gianinazzi S, Barea JM, et al. (2002) Localized versus systemic effect of arbuscular mycorrhizal fungi on defence responses to Phytophthora infection in tomato plants. J Experimental Botany 53: 525-534.

61. Rengel Z (2002) Genetic control of root exudation. Plant and Soil 245: 59-70.

62. Haichar FeZ, Marol C, Berge O, Rangel-Castro JI, Prosser JI, et al. (2008) Plant host habitat and root exudates shape soil bacterial community structure. ISME J 2: 1221-1230.

63. Hartmann A, Schmid M, Tuinen Dv, Berg G (2009) Plant-driven selection of microbes. Plant and Soil 321: 235-257.