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Potential of New *Prunus* Rootstocks for Managing *Armillaria* Root Rot Disease in Peach Production

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Abstract

Armillaria root rot (ARR) pathogen is currently one of the most important diseases affecting peach [*Prunus persica* (L.) Batsch] production in the southeastern United States causing high plant mortality. This soil-borne disease affects the roots of the plant, producing subsequent symptoms in the canopy, and finally killing the host. No chemical control is currently available for ARR. To overcome this disease, rootstock use is an option; however, resistant rootstocks are fairly new and their availability is limited. The objective of this review is to describe the sources of resistance against the pathogen, the rootstock breeding procedures for peaches, and the management tools for fighting the infection and reducing symptoms. Multiple peach and plum accessions have been evaluated for ARR resistance over the last few decades. The main sources of resistance were identified in plum hybrids of native North American plum species. These resistance sources were used as the foundation for breeding peach rootstocks with resistance to ARR. Resistant plum lines were hybridized with peach germplasm to develop rootstocks resistant to ARR. Two rootstock cultivars were developed and released: 'Sharpe' and 'MP-29'. Although some ARR disease management practices have been examined, rootstocks are still a good option to reduce losses induced by ARR in peaches.

Armillaria fungi overview. Armillaria root rot (ARR) is naturally present in forests (Wargo and Shaw III, 1985). The disease is mainly found in temperate and tropical areas of the world, and in almost every state in the United States (Williams et al., 1986). It is caused by different species within the fungal genus *Armillaria,* such as *Armillaria tabescens* (Scop) Emel, *Armillaria mellea* (Vahl:Fr) Kummer, *Armillaria ostorya* (Romagn.) Herink, *Armillaria gemina* Bérubé & Dessureault, *Armillaria calvescens* Bérubé & Dessureault, *Armillaria sinapina* Bérubé & Dessureault, *Armillaria gallica* Marxmüller & Romagn., *Armillaria nabsnona* Volk & Bursdall, and *Armillaria cepistipes* Velenovsky (Williams et al., 1986; Cox et al., 2005; Volk and Burdsall, 2016). In the southeastern United States, *A. tabescens* is the main species causing ARR, followed by *A. mellea* (Schnabel et al., 2005). Classified as basidiomycetes (Smith et al., 1990), these fungi can behave as primary pathogen, negatively affecting plant growth, leaving plants susceptible to attack by various pathogens and insects. This behavior occurs mainly in inland coniferous forests of the Western United States, a relatively dry region (Williams et al., 1986). Besides acting as a primary pathogen, ARR can be a secondary pathogen in stressed plants (because of competition, pests, and adverse climatic conditions for example) and even behave as a saprophyte in decomposing dead trees (Wargo and Shaw III, 1985).

The life cycle of most *Armillaria* species involves a parasitic phase, which is characterized by the fungi invading the host, and the saprophytic phase, which is characterized by utilizing the host as food for its development (Morrison, 1976). The parasitic phase of ARR starts by spreading through rhizomorphs which are root-like fungal structures (Wargo and Shaw III, 1985; Williams et al.,

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1986). Rhizomorphs start the colonization process by penetrating the outer layers of the host's root, mainly in root sections that have suffered stress or necrosis. Further, as the mycelial fans grow during the saprophytic phase and the necrotic area increases, the infection may reach the cambial zone inducing the decay of the root. After colonizing one plant, the rhizomorphs will grow and reach other plants. These additional plants may be affected by the fungi depending on the specific health and conditions of the new plant (Morrison, 1976; Wargo and Shaw III, 1985). However, some differences in the life cycle are seen in the southeastern United States. Rhizomorphs are rarely produced and the disease spreading is primarily through contact among peach roots and old infected root pieces left in the soil from previous orchards/forests. Mushroom spores coming from adjacent forests contribute little to the disease spreading (Cox et al., 2005)

The detection of an *Armillaria* infection is difficult because the initial plant symptoms occur underground (Williams et al., 1986). However, as the infection progresses, the plant canopy starts to display symptoms like foliage discoloration (chlorosis, sometimes bronzing of foliage and branches), branch dieback, and plant growth reduction (Cox et al., 2005; Morrison, 1976; Williams et al., 1986).

Importance of ARR in peach production. One of the main causes of premature tree mortality in stone fruit orchards in the southeastern United States is ARR (Cox et al., 2005) (Fig. 1), followed by peach tree short life (PTSL) (Fig. 2) (Clemson Cooperative Extension, 2015). ARR is a devastating disease (Fig. 3); however, no chemical control is feasible because of the high persistence of ARR in the soil (Myers and Bennett, 1989; Evert and Bertrand, 1993; Beckman, 1998), leaving few options to control the disease (discussed below). The high disease persistence inhibits the establishment of new

Fig. 2: Peach tree killed by PTSL. Courtesy of T. Beckman.

Fig. 1: Peach tree plans collapsing due to ARR infection. Courtesy of T. Beckman.

Fig. 3: Commercial peach orchard devastated by ARR. Courtesy of T. Beckman.

orchards in previously cultivated land, adding additional costs for the peach industry (Clemson Cooperative Extension, 2015).

The first symptom of ARR infection is below the soil's surface with root necrosis causing roots to have a spongy consistency. White to yellow fungi mycelial fans can be observed by cutting through the bark (Fig. 4). Rhizomorphs may grow in infected tissues. Under favorable environmental conditions, the reproductive fungal structures (basidiocarps) may emerge from the base of the trunk or from shallow roots around the infected trees. After severe infection of the root system and plant crown, cracks or wounds in the bark can exude gum, and leaves can become chlorotic, underdeveloped, curled, and wilted. Subsequently, individual limbs and branches will die as the disease progresses. Eventually, the entire plant will die (Cox et al., 2005).

Breeding for ARR resistance: Possible germplasm sources and its utilization. The genus *Prunus* L. is composed of approximately 100 species, subspecies, and varieties of peaches, plums, cherries, almonds, nectarines, and apricots (USDA Natural Resources Conservation Service, 2015). Members of this genus can be found in most of the United States (Ramming and Cociu, 1991).

Native *Prunus* species are potential sources of beneficial genetic material with inherit variation for disease and insect resistances, which could be beneficial for the improvement of either fruiting cultivars or rootstocks (Blažek, 2007; Hancock, 2008). Additionally, these materials may also offer useful contrasts in chilling requirement and cold hardiness (Beckman and Okie, 1994).

At the beginning of the 19th century, native North American plum species, such as *Prunus americana* Marsh., *P. hortulana* Bailey, *P. angustifolia* Marsh., *P. besseyi* Bailey, *P. nigra* Ait., and *P. munsoniana* Wight & Hedrick and their hybrids, were commonly utilized as fruiting cultivars (Beckman and Okie, 1994). However, following the introduction of Japanese and European lines with

Fig. 4: Mycelial mat beneath bark in ARR infected peach tree. Courtesy of T. Beckman.

their perceived superior handling and eating qualities, the utilization of cultivars developed from native North American species declined (Ramming and Cociu, 1991). This trend has recently reversed, and now, in addition to the species utilized at the beginning of the 19th century, additional germplasm is also used, such as *P. salicina* Lindley, *P. cerasifera* Ehrhart, *P. pumila* L., *P. subcordata* Benth, and *P. mexicana* S. Watson (Beckman and Okie, 1994). These different species provide distinct useful traits that are not found elsewhere (Norton et al., 1990, 1991a, 1991b; Okie et al., 1992; Layne, 1994; Nicotra and Moser, 1997; Grzyb et al., 1998; Lu et al., 1998; Lecouls et al., 1999; Stefani, 2010)

Trait characterization in different species has helped identify the best germplasm for use in breeding programs with the aim to generate lines and cultivars with new and superior characteristics. For example, efforts have been made over the last two decades to develop an ARR-tolerant rootstock for peach production (Beckman et al., 1998, 2008; Beckman and Pusey, 2001; Reighard, 2002; Beckman, 2011).

Reighard et al., (1997) evaluated 37

Prunus rootstock cultivars and advanced selections in six locations in South Carolina over multiple years. Various species and sources of germplasm were used, such as peach and hybrid plum rootstocks. The objective of the research was to evaluate tree vigor, longevity, disease resistance, and yield of commercial cultivars grafted onto different rootstocks. As expected, there were useful variations within the rootstocks. Rootstocks bred to tolerate non-fumigated replant PTSL areas performed better than the others. However, European rootstocks did not perform well in South Carolina soils. These results illustrated the effect of environmental variation and the genotype by environment interaction on many commercial traits.

A large cooperative regional trial was established in 1983 (Beckman et al., 1998) to test the survival of more than 100 lines of *Prunus*, including peaches and plums (Fig. 5). They reported that the main cause of plant mortality was PTSL (50%), followed by ARR (35%). Further examination of the results indicated that some plums were the least affected by ARR. Plum hybrids with North American plum species in their genetic background were among "the best lines", while the lines without North American plum ancestry were among "the worst lines". In the same report, the authors stated that although

Fig. 5: High density trial to evaluate peach trees resistance to PTSL and ARR. Courtesy of T. Beckman.

Fig. 6: Bronzing of foliage due to the grafting incompatibility of peach on a hybrid plum rootstock. Courtesy of T. Beckman.

some plums showed potential as rootstocks for peach, most of the plums displayed variable grafting compatibility with commercial peach cultivars, thereby limiting their direct use as rootstocks (Fig. 6). Efforts were undertaken to utilize the resistant plum germplasm via crossbreeding with peach lines in order to improve graft compatibility.

Several other sources of resistance for ARR were reported. Thomas et al. (1948), detected resistance to ARR in different plum lines in California. Proffer et al. (1988) tested different cherry rootstocks in Michigan for ARR infection. Guillaumin et al. (1991) investigated the level of ARR resistance in different rootstocks originated from plums. Loreti (1997), recommended plum rootstocks based on several traits, including resistance to ARR.

Rootstock development. Historically, peach seedlings have been used as rootstocks for commercial peach production (Layne, 1987); however, seedlings are not uniform. Breeding programs have started to focus on developing rootstocks adapted for specific regions and conditions in the United States (Reighard, 2002). For example, in an effort to understand the genetics of PTSL, Blenda et al. (2007) crossed a PTSL resistant rootstock (Guardian) with a susceptible rootstock

Fig. 7: Greenhouse grown rootstock seedlings destined for field. Courtesy of T. Beckman.

Fig. 8: Nursery grown rootstock seedlings being prepared for tests in the field. Courtesy of T. Beckman.

(Nemaguard). The objective was to evaluate the segregating population for PTSL syndrome, and to develop a genetic linkage map for peach rootstocks.

The United States Department of Agriculture, Agricultural Research Service (USDA-ARS), located in Byron, GA houses the peach rootstock breeding program for the southeastern United States. The first evidence of resistance to ARR was reported by Beckman et al. (1998) in this breeding program. The resistant lines were used as parents in crosses, and with the addition of other sources of resistance, superior parents were generated and utilized to develop new hybrids resistant to ARR (Beckman, 2011) (Fig. 7, 8, and 9).

One of the first ARR-resistant rootstocks released for peach production was ‘Sharpe’, a clonal plum rootstock (Beckman et al., 2008) (Fig. 10). The pedigree of ‘Sharpe’ is unknown. ’Sharpe’ appears to be a hybrid of *P. angustifolia* with an unknown plum species. Furthermore, this rootstock is also resistant to PTSL and some root-knot nematodes. Despite that, as trees aged, yields of ‘Redhaven’ peach on ‘Sharpe’ declined when compared with trees grafted onto ‘Guardian’ (Fig. 11) (Beckman et al., 2008). ‘Sharpe’ is a potential source of disease resistant genes for peach rootstock breeding (Beckman and Chaparro, 2015). ‘Sharpe’ can be propagated by softwood or hardwood cuttings. ‘Sharpe’

Fig. 9: High density field trial of advanced rootstock selections. Courtesy of T. Beckman.

Fig. 10: ‘Sharpe’ clonal plum rootstock for peach. Courtesy of T. Beckman.

Fig. 11: Guardian peach seedling rootstock. Courtesy of T. Beckman.

Fig. 12: 'MP-29' clonal interspecific hybrid peach rootstock. Courtesy of T. Beckman.

was not patented and is publicly available for research, cultivar development (Beckman et al., 2008), and homeowner production.

The most recent rootstock release resistant to ARR was 'MP-29', a clonal interspecific plum-peach hybrid rootstock for peach (Beckman et al., 2012). 'MP-29' was selected in a 1994 cross of a hybrid plum species ('Edible Sloe') and an advanced peach rootstock selection ('SL0014') (Beckman et al., 2013). 'MP-29' was released as a superior ARR, PTSL, and nematode resistant rootstock (Beckman and Chaparro, 2015). 'MP-29' induces equal if not superior yields of 'Redhaven' peach, compared with trees grafted onto 'Guardian' rootstock (Beckman et al., 2012). 'MP-29' can be propagated through softwood or hardwood cuttings and tissue culture. 'MP-29' was patented in 2013 using The Florida Foundation Seed Producers, Inc. as the licensing agent. Peach trees grafted on 'MP-29' are currently commercially available in small numbers due to its recent release and due to its different propagation and grafting scheme from the traditional seed propagated rootstock. Commercial trials comparing 'Guardian' and 'MP-29' in ARR infested soils can be located across southeastern Unites States. Until now, 'MP-29' trials show increased survival and comparable performance to trees grafted onto 'Guardian' rootstocks. 'Sharpe' and 'MP-29'

Fig. 13: 'MP-29' clonal interspecific hybrid peach rootstock grafted with 'Julyprince' peach. Courtesy of D. Chavez.

rootstocks have been tested for graft compatibility with several scions other than 'Redhaven', and have shown no signs of incompatibility (Beckman et al., 2008, 2012).

Disease management. The use of rootstocks resistant to ARR is a feasible avenue for disease management. Two rootstock cultivars have been released - 'Sharpe' and 'MP-29' – and are an excellent alternative for cultural management for ARR. 'Sharpe' trees are currently recommended for homeowner production due to its yield decline as trees aged in comparison with standard rootstocks. 'MP-29' is recommended for commercial production; however, commercial trials are still in early stages of evaluation. No known adverse characteristics have been identified in 'MP-29' compared with 'Guardian' rootstocks (Beckman, personal communication).

There are only a few cultural management options for ARR, and most are not effective or need more study in commercial settings. Baldi et al. (2015) tested the effects of Brassica seed meal on *A. mellea* growth *in vitro* and *in vivo*. *A. mellea* growth was reduced *in vitro*; however, there was not enough infection symptoms in potted trees (*in vivo*) to conduct the experiment. The authors suggested that *Brassica* derivatives have a potential activity against *A. mellea* (based on the *in vitro* studies). Schnabel et al. (2012) tested root collar excavation in peach trees planted in two ARR infested sites. Peach trees were initially planted directly in the ground (as the standard growers' method) or in open-bottom Smart Pot (fabric pot of 45 cm height by 60 cm diameter). Eight months later, roots were excavated in order to expose and evaluate the root collar. Five years after planting, approximately 50% of the plants grown as the standard growers' method died due to ARR infection and only 5% of the plants grown with the excavated root collar died. The authors indicated this prototype as a potential option for ARR management, maintaining vigorous plants as the control plots. In another study, Schnabel et al. (2011) drenched *Trichoderma spp.* onto peach trees after planting and biannually (spring and fall) for three years. Plants were grown in commercial orchards on replant sites previously infected with ARR. No significant differences were found on tree survival between the treated and non-treated plants, and trunk diameter was greater for treated plants compared to non-treated plants three and four years after planting. The results indicate that *Trichoderma spp.* is ineffective to control ARR infection in peaches.

Cox and Scherm (2006 tested five species of saprobic (*Ganoderma lucidum*, *Hypholoma fasciculare*, *Phanerochaete velutina*, *Schizophyllum commune*, *and Xylaria hypoxylon*) in combination with *A. tabescens* and *A. mellea* with the objective of assess if the five species would exclude *Armillaria* from peach roots. The experiments were conducted using glass slides, wood blocks, and root pieces in controlled conditions in the laboratory. *G. lucidum, S. commune, and X. hypoxylon* reduced *Armillaria* growth above and below the bark. The authors speculated that these three species are good candidates for future field tests in peach orchards.

Chemical treatment to fight ARR infection is not feasible in commercial orchards due to the nature of the disease. Research on soil fumigation and drenches produced inconclusive results and field tests were not extensively conducted (Clemson Cooperative Extension, 2015). Amiri et al. (2008) tested six different chemical groups of fungicides to control ARR, showing some promising results. The objectives were to evaluate the fungicides' efficiency against *A. tabescens* isolates in vitro, and the activity of these fungicides in peach roots and trunk after intravascular infusion. Propiconazole was the most effective group inhibiting mycelial growth of the isolates. Furthermore, propiconazole was detected in primary roots and trunk segments of peach plants, indicating that after infusion, the fungicide was able to move in the plant. These results suggested that propiconazole can be used as a management option against *A. tabescens*. Adaskaveg et al. (1999) tested different terapeutic treatments of sodium tetrathiocarbonate (STTC) and propiconazole to manage ARR in almond plants grafted onto peach rootstocks in laboratory and field conditions. Single-season treatmens of STTC in infected mature trees did not prevent tree mortality caused by ARR. ARR infected trees treated with propiconazole had a 2-year life span, whereas plants not treated died within 4 months. Propiconazole reduced mycelial growth of *A. mellea* by 50%, in laboratory studies.

Summary

The use of ARR resistant rootstocks remains the main option to control ARR infection in peaches. The development of these rootstocks is an important step towards sustainable peach production in the southeastern United States, increasing tree longevity in peach orchards. Through the use of native plum lines in hybridizations, ARR resistant rootstocks were released and have been used with proven ability to produce high yields while avoiding ARR infection. Breeding efforts targeting ARR are currently in place in public and private institutions, foreseeing the production and availability of resistant material for future tests and uses.

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