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Review

Rootstocks for Commercial Peach Production in the Southeastern United States: Current Research, Challenges, and Opportunities

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Abstract: The Southeastern United States is facing agriculture crises, such as the ongoing epidemic of citrus greening disease that has forced the region to begin looking into alternative crops. Some of these belong to the Rosaceae genus *Prunus*, which encompasses many economically important species such as peaches, almonds, cherries, plums, and more. Peach production in Florida has become a very promising alternative to citrus; however, there are different limitations and challenges that peach production faces in this region. Differing climates coupled with edaphic challenges such as salinity, alkalinity, and waterlogging have been the focus of much of the research into the viability of peach production in the region. Using the genetic diversity of the *Prunus* genus is crucial to the success of peach as an alternative crop, due to the nature of its propagation on rootstocks. The development of new rootstock cultivars has been—and continues to be—the most efficient way not only to deal with the variety of problems associated with the climate and soil mentioned above but also to mitigate the effects of pests and diseases. The vegetative propagation of stone fruit rootstocks also has distinct advantages that seed propagation cannot achieve, including tree performance uniformity and the multiplication of interspecific hybrids. Tools used to select the best-performing rootstocks for the area such as the root system architecture (RSA) analysis are fundamental to this development process to ensure that the rootstock cultivars with the traits needed for success in the region are selected. This narrative review lays out all the challenges facing southeastern peach production in detail, discussing the research into these challenges and highlighting the tools that are most crucial to the success of peach production in the region to create a resource for researchers, growers, and breeders to more easily access this information.

Keywords: peach; rootstocks; Southeast United States; stone fruit

1. Origin and Characteristics of Peach and Almond

Prunus is a genus from the Rosaceae family that encompasses about 230 species [1] that are widely distributed across the world. Three-quarters of the *Prunus* species are native to Asia, Europe, and North America [2], and the remaining other species are native to the subtropical and tropical forests of Asia, Africa, South America, and Australia [3]. The genus exhibits considerable ecological diversity, with different species occurring from lowlands to alpine zones and in wet and dry forests, as well as deserts [4]. There are deciduous and evergreen species, trees, and shrubs considered economically important fruit and nut crops, such as peaches, *P. persica*, and almonds, *P. dulcis*. According to the most widely accepted infrageneric classification of *Prunus*, peaches and almonds belong to the same subgenus: *Amygdalus* [2]. Successful hybrids have been produced between peaches and almonds, among others such as apricots, plums, and sour cherries. In most cases, these interspecific hybrids are largely sterile, although the F_1 of almonds and peaches can be highly fertile and can be employed as rootstocks for both species [1].

The modern *Prunus* appeared ~61 million years ago in Eastern Asia, and its global distribution and diversification were shaped by a complex interplay of geologic tectonic events and climatic oscillations [5]. It has been suggested that climatic change was likely a driver for *Prunus* diversification during the Paleocene–Eocene Thermal Maximum event. According to Bayes-DIVA (Bayesian Dispersal-Vicariance Analysis), a method for inferring the distributional history of organisms, the centers of diversity for *Prunus* crop lineages (e.g., plums, cherries, peaches, and almonds) are found chiefly in Eurasia. The most common recent ancestor of *Amygdalus* was widespread from West Asia to Eastern Asia (China) ~50 million years ago, with a subsequent diversification into almonds in West Asia and peaches in Eastern Asia [5]. A tectonic collision of the India plate with Eurasia ~50 million years ago brought about orogenic uplifts of the Tibetan Plateau that could likely contribute strong vicariance forces in shaping the diversification process [5,6].

2. Economic Importance of Peaches in the United States

Peaches are one of the major stone fruits worldwide [7], the United States being the world's sixth-largest peach producer, behind China and the European Union. Peaches are commercially produced in 20 states of the United States [8]. California is the top peach-producing state, accounting for approximately 70% of the domestic production, followed by South Carolina, Georgia, and New Jersey [9]. The bearing acreage of peach trees in the United States has been gradually declining for the past two decades [8]. The reasons for this decline are not clear and differ across the country according to area-specific situations. Among the reasons, we find farmers unwilling to renew their orchards, unpredictable weather patterns, and deadly diseases [10,11]. In 2016, there was an estimated area of 37,583 ha of peaches with an estimated yield per ha of 21.07 (tons fresh equivalent) [8]. By 2020, the production area went down to 29,542 bearing ha with an estimated yield per ha of 20.91 (tons fresh equivalent) [12].

The Florida peach industry is relatively new, although growers have experimented with growing peaches in Florida for decades. Despite the small Florida peach industry, it has been growing, increasing the harvested hectares from 500 in 2012 to 1200 in 2014 [13]. Peaches have become a relevant specialty crop in Florida and a promising alternative that may help the profitability of growers of traditionally cultivated crops such as citrus. This emerging importance is evidenced in the increasing peach acreage in Florida, whereas the cultivated area at the national level has been decreasing during the last decade [8,9,14]. Currently, the industry is valued at more than USD 10 million annually and produces 3.3 million kg of fruit [14].

Growing peaches in Florida has been identified as a potential alternative crop for citrus farmers who have lost groves due to Huanglongbing disease (*Candidatus* Liberibacter asiaticus). The peach production region with the earliest potential harvest dates is located in Central and South Central Florida, where citrus was once prevalent [15]. With this objective in mind, research has focused on the breeding and evaluating low-chill peach cultivars suitable for Central and South Florida. The stone fruit breeding program in Florida has focused on releasing non-melting-flesh peaches for the fresh market [16]. On the other hand, later-maturing cultivars have little or no potential in Florida because of increased market competition and increased pest and disease pressure [17]. Therefore, the development of early ripening low-chill cultivars has enabled Florida growers to grow and harvest peach fruit during late March and early April, when there are higher prices, prior to other states such as Georgia, California, and South Carolina [18]. Furthermore, the breeding program has been developing numerous cultivars and rootstocks adapted to Florida's environmental conditions with additional promising traits such as root-knot nematode resistance [19].

3. Rootstocks for Stone Fruit Production

Stone fruit trees for commercial production are typically propagated on rootstocks, given that the rootstock can provide the scion with benefits such as resistance to pests and pathogens. The choice of rootstock is as crucial as the scion, because it determines whether the trees can survive and grow under unfavorable edaphic conditions, such as a high bulk density, coarse texture (sand), parasitic nematodes, fungal and oomycete pathogens causing root rot, high pH, or other orchard replant problems [20]. Rootstocks can also influence the scion vigor and positively affect the precocity, crop efficiency, fruit size, and quality [21]. Many stone fruit species can be budded on other *Prunus* species, and the range of rootstocks now available for peach production worldwide has increased dramatically [20]. Several factors have prompted international research to focus on developing new rootstocks suitable for the needs of modern peach production [5].

Rootstock breeding is relatively recent. Until the first half of the 20th century, rootstocks were generally selected from random seedling populations, choosing the individuals mainly because of their good propagation abilities [22]. Significant progress was made by rootstock breeders in the second half of the 20th century [23], with increasing interspecific hybridization to combine desirable traits in a single rootstock [24]. Interspecific hybrids between different *Prunus* species (i.e., peaches × almonds) confer traits that peaches lack, such as growing in nonoptimal and low-chill areas, adaptation or tolerance to heavy soils, waterlogging, alkalinity, drought, reduction of canopy vigor, allowing for an increase in planting densities, and soil fungal diseases and nematodes [25]. Many new rootstocks and breeding projects have contributed to widening the knowledge in genetics and the inheritance mechanisms of rootstock traits and the physiology of rootstock/scion interactions. However, additional information on the genetic diversity and heritability of rootstock characteristics of species such as plums or peaches is still needed [23].

Peach rootstocks in the United States are almost exclusively open-pollinated seedlings of *P. persica*. Currently, these peach seedlings, derived primarily from the rootstock cultivars 'Lovell', 'Halford', 'Nemaguard', 'Nemared', 'Bailey', and 'Guardian'^{TM}, this last as currently the most propagated rootstock in the Southeast United States [20].

4. Production Problems in Southeast United States (Potentially Solved with Rootstocks Breeding)

4.1. Biotic Stress

4.1.1. Peach Tree Short Life (PTSL)

Peach Tree Short Life (PTSL) is an economically important disease that affects several *Prunus* species. Affected trees wilt, collapse, and die suddenly. PTSL is most common in sandy soils [26], such as most of Florida's soils. PTSL is a disease complex caused by the initial attack of ring nematode (*Mesocriconema xenoplax*), making the plant more sensitive to cold temperature fluctuations and to bacterial canker (*Pseudomonas syringae* pv. *syringae*) [26]. Interestingly, other nematodes such as root-knot nematode (*Meloydogine incognita*) do not play a role in PTSL [27].

PTSL symptoms occur at the aerial part of 3–6-year-old trees, in which sap oozes out of scaffold limbs and the trunk [26,27]. The sudden collapse occurs during or just after blooming, despite the tree apparently being healthy in the previous fall, because cambial vascular tissue dies, affecting the tree's capacity to transport water and nutrients [28]. The bacterial canker infection does not extend beyond the soil line, leaving the primary root system alive and allowing suckers to arise from the tree's base during the summer [26].

Since ring nematode is one of the initial agents that generate PTSL, and preplant fumigation is expensive and does not provide long-term control of these parasitic pathogens, the selection of tolerant/resistant rootstocks is one of the most effective management strategies against PTSL. Additionally, the type of scion influences the incidence of PTSL, since the rootstock performance depends on its interaction with the scion [29].

'Lovell' and 'Nemaguard' are two peach rootstocks susceptible to PTSL, especially 'Nemaguard', which allows the aboveground depletion of nutrients, since this translocates carbohydrate reserves from shoot to root in response to a ring nematode attack [20,28]. Therefore, 'Nemaguard' should be avoided as a rootstock in soils with a ring nematode presence. On the other hand, 'Guardian'™ is a rootstock that traces its lineage back four generations to a 'Nemaguard' cross in 1954. It exhibits a higher tolerance to ring nematode, bacterial canker, and PTSL than 'Lovell' and 'Nemaguard' [20]. However, 'Guardian'™ is not immune to PTSL and only performs satisfactorily in conjunction with the best management practices for suppressing the disease [28].

4.1.2. Oak Root Rot (*Armillaria mellea*)

Armillaria spp. is a genus of fungi that attacks forest species and cultivated woody plants such as peach *P. persica* and avocado (*Persea americana*). About 129 species have been identified and distributed in almost all the continents (MycoBank: http://www.mycobank.org/; accessed on 2 July 2022). In North America, there are three species of *Armillaria* spp. associated with peaches: *A. mellea*, *A. ostoyae*, and *A. tabescens* (syn. *Clitocybe tabescens*) [26]. *Armillaria* spp. can colonize the remaining roots after removing the infected trees from the orchard, while the oomycete pathogen *Phytophthora* spp., a causal agent of peach root rot, develops in poorly drained soils [30].

Unlike *Phytophthora* root rot, *Armillaria* develops in well-drained soils, and in contrast to PTSL, root suckers do not emerge from the rootstock crown. The early symptoms of oak root rot include poor terminal growth and undersized, curled leaves, and the tree may collapse suddenly during the summer, with most of the leaves still attached [26]. In advanced stages of the disease, the cellulose, hemicellulose, and lignin degradation turns the wood soft, spongy, and white [31] (Figure 1A). Despite the sudden appearance of the symptoms, the disease typically takes a long time, even years, to kill the tree. One of the most characteristic signs of *Armillaria* infection is the growth of white mycelial fans at the base of the tree in the cambium between the bark and wood (Figure 1B).

Oak root rot is difficult to control, since the fungus can colonize the remaining root pieces after removing the infected trees from the orchard [30]. Additionally, chemical control is not entirely effective [32], and the frequent application of chemical fungicides can induce resistance in the pathogen in the long term.

The selection of resistant rootstocks is one of the most recommended strategies to control oak root rot [20]. It has been found that many *Prunus* spp. are susceptible to *Armillaria* spp., such as the sections *Amygdalus* (peaches, almonds, Tibetan peaches, Gansu peaches, and Chinese wild peaches); *Armeniaca* (apricots); *Cerasus* (sweet cherries, sour cherries, and St. Lucie cherries); Western sand cherries; and their hybrids. However, there are tolerant species that belong to the sections *Euprunus* (*P. domestica*, *P. insititia*, *P. cerasifera*, and *P. spinosa*) and maybe *Prunocerasus* (*P. subcordata* and *P. munsoniana*) [33]. These materials are tolerant, because they exhibit post-infection reactions, where anthocyanins are synthesized as an antifungal compound that prevents mycelia from growing. 'GF-677' rootstock (*P. persica* × *P. dulcis*) responds to infection by rapidly replacing the roots affected by the disease [33]. Beckman et al. [34] reported that the rootstock 'Sharpe' (plum hybrid) and the rootstock 'MP-29' [35], an inter-specific plum × peach hybrid, to be resistant to *A. tabescens*. Additionally, Baumgartner et al. [36] found that the rootstock 'Myrobalan' plum (*P. cerasifera*) and its interspecific hybrids are resistant to *A. mellea* and *A. tabescens*. Unfortunately, 'Myrolaban' plum has compatibility problems with peaches, especially in sandy soils, similar to most Florida soils. Elias-Roman et al. [37] found that 'Mondragon' rootstock (*P. salicina*) has a high resistance to *A. mexicana*, with the lowest infected roots incidence and no infection by *A. mellea* under greenhouse conditions.

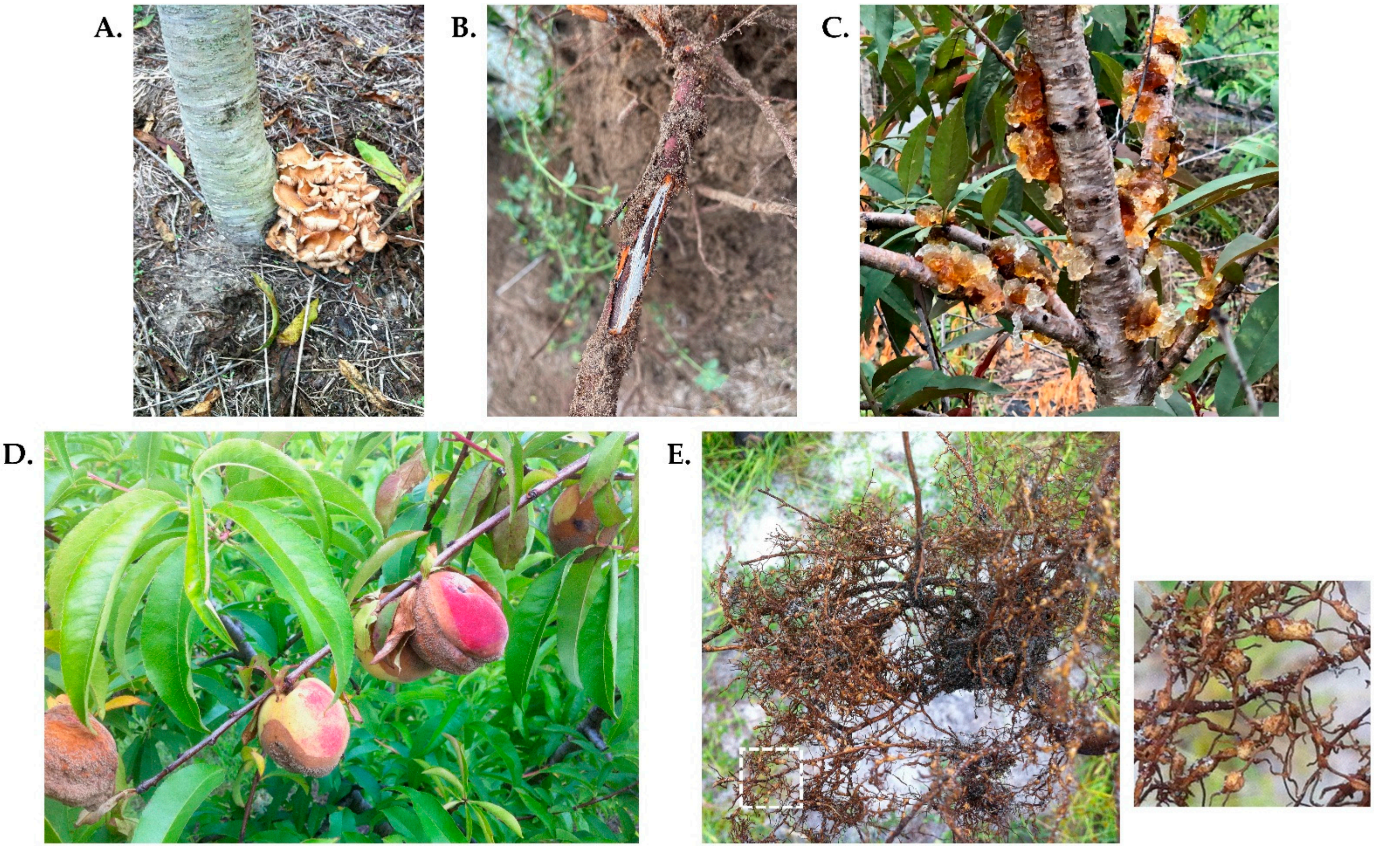

Figure 1. (**A**) Oak root rot disease in peaches caused by *Desarmillaria mellea* with typical fan-shaped mycelial mats at the base of the tree. (**B**) White mycelia of *Desarmillaria mellea* growing underneath an anchorage root bark. (**C**) Peach gummosis disease caused by *Botryosphaeria dothidea* in an infected tree, with limbs exuding large amounts of gum. (**D**) American brown rot disease caused by *Monilinia fructicola* developing on ripening fruit and foliage. (**E**) Root-knot nematode galls caused by *Meloidogyne* spp. in an infected young peach tree. Photos courtesy of Jose X. Chaparro.

4.1.3. Root-Knot Nematodes (*M. floridensis*, *M. arenaria*, and *M. javanica*)

The causal agents behind root-knot disease (RKN) belong to the *Meloidogyne* genus. *Meloidogyne* spp. are obligate plant endoparasitic nematodes that penetrate plant roots and suck the nutritional resources, causing root galling symptoms generated by giant feeding cells and division of the surrounding vascular parenchyma cells [38] (Figure 1E). Additional aboveground symptoms include the reduction of tree vigor and early defoliation, which ultimately results in yield reduction. The symptoms are enhanced in sandy soils, especially when trees are exposed to drought conditions [27]. The three predominant *Meloidogyne* species that affect *Prunus* species are *M. arenaria*, *M. incognita,* and *M. javanica*, all of which are polyphagous and reproduce exclusively by parthenogenesis [27].

In Florida, another species, *M. floridiensis*, was identified by Sharpe et al. in 1966, parasitizing 'Okinawa' and 'Nemaguard' rootstocks, which are resistant to *M. incognita* and *M. javanica*. Compared with the others, *M. floridiensis* exhibits different body lengths and anatomy, facultative meiotic parthenogenesis, and creates smaller galls [39].

The resistance of Myrobalan plum (*P. cerasifera*) is attributed to three major genes, Ma1, Ma2, and Ma3, which confer high and wide-spectrum resistance to all the predominant RKN species, such as *M. arenaria*, *M. incognita*, *M. javanica,* and *M. floridiensis* [40]. The genes Ma1, Ma2, and Ma3 were identified in the Myrobalan clones 'P.2175', 'P.1079', and 'P.2980', respectively [41]. Lecouls et al. [42] suggest that Ma1, Ma2, and Ma3 could be closely linked to three allelic forms of the same gene: Ma. The Ma gene is used directly or through interspecific hybrids for rootstock breeding in stone fruits using MAS [43].

The full-length cDNA (2048 amino acids) of Ma is one of the longest of all the resistance genes cloned to date and the first cloned gene for resistance to RKN in a perennial crop species. Another major feature of interest of Ma is that RKN resistance is not affected by high inoculum pressures [44].

Plant-parasitic nematodes reduce 10–12% of the global crop production on average [45], and the *Meloidogyne* spp. is one of the most economically important nematode genera in *Prunus* [27]. More than 90 species of *Meloidogyne* spp. have been identified and are distributed in temperate, tropical, and equatorial areas [26].

Since most of the nematicides are being progressively removed from the market, the use of resistant rootstocks for managing *Meloidogyne* spp. in *Prunus* is the most economical and environmentally sound method [27]. In this regard, rootstocks from the subgenus *Amygdalus* (Chinese wild peaches, peaches, almonds, or peach × almond hybrids) have been developed to confer resistance to *Meloidogyne* spp. Peach cultivars, such as 'Nemaguard', 'Nemared', and 'Okinawa', were selected in the United States from the 1960s onwards for additional resistance to *M. javanica* [46]. Similarly, resistance has been identified in several plum rootstocks, including *P. insititia*, *P. spinosa*, and *P. domestica*. Some 'Myrobalan' plum clones express a complete resistance to more than 30 *Meloidogyne* spp. [47]. Some resistance mechanisms consist of hypersensitivity to juvenile nematodes; other mechanisms allow the juvenile nematodes to penetrate and form small galls but prevent maturation and reproduction. This last has been observed in 'Okinawa' and 'Nemared' rootstocks with *M. javanica* and in 'Guardian'™ with *M. incognita* [27]. Finally, in 1991, the peach rootstock 'Flordaguard' was released with resistance to *M. floridensis*, a trait that 'Nemared', 'Nemaguard', and 'Okinawa' lacked. This resistance in combination with a lower chill requirement made it the most popular rootstock in Florida.

4.1.4. Peach Gummosis Caused by *Botryosphaeria dothidea*

Peach gummosis is an important disease caused by *B. dothidea*, which affects a large number of hosts worldwide. *B. dothidea* is particularly virulent on peach trees, with an estimated yield reduction of up to 40% in severe cases [48]. The disease was first reported on peaches and citrus in Florida by Fawcett and Burgerin in 1911 and has spread since the 1970s throughout the Southeastern United States [49], where the climatic conditions are conducive to peach gummosis.

B. dothidea overwinters in diseased bark and woody tissues, and the infections can occur through wounds, pruning cuts, and natural openings such as stomata and lenticels. Under wet conditions, abundant conidia (asexual spores) may be produced and disseminated through irrigation splash and wind-driven rain [50]. After infection, most symptoms appear in the spring and the beginning of the summer, when the temperature increases [51].

Infected trees are weakened, exhibiting a dieback of twigs, shoots, and even limbs, and exude large amounts of gum. Gum exudates on the trunk and main scaffolds have been used to measure disease incidence and severity [49] and serve to identify the differences in susceptibility to peach gummosis on rootstock cultivars [48] (Figure 1C).

Currently, there is no chemical control for peach gummosis. For example, Captan™ does not provide a sustained suppression of the pathogen, and Captafol™ performs efficiently [49], but it is no longer registered for use on peaches. For these reasons, resistant cultivars are the most recommended strategy for peach gummosis control [48]. However, none of the cultivars currently utilized in Florida display valuable resistance levels, which is why fungal gummosis resistance is one of the goals of ongoing breeding efforts. A genetic source for resistance to peach gummosis was identified recently in 'Tardy Nonpareil' almonds [52].

4.1.5. Diseases Caused by *Xylella fastidiosa*

X. fastidiosa is a non-flagellated Gram-negative bacterium that proliferates only in xylem vessels in roots, stems, and leaves, moving down- and upstream in the plant. Its optimal growth occurs at 26–28 °C and is transmitted persistently by xylem sap-sucking insects [53,54]. This bacterium has a very wide variety of host species, where the main fruit tree hosts of economic importance are:

1. Grapevine (*Vitis vinifera*): causes Pierce's Disease (PD). In this species, *X. fastidiosa* was first identified at the end of the 19th century in the U.S. The first symptoms are sudden drying of large parts of green leaves that later become necrotic at the leaf margins before finally dropping. In general, these symptoms can be confused with salt toxicity or a deficiency of boron (B), copper (Cu), or phosphorus (P). Defoliation, shoot dwarfing, and cane stunting, as well as the dehydration of fruit clusters, may occur.
2. *Citrus* spp.: causes Citrus Variegated Chlorosis (CVC) or Citrus X Disease. Symptoms can be observed, especially on sweet orange trees from the nursery up to 10 years old, as small interveinal chlorotic spots on leaves, similar to Zn deficiency. The fruits remain small, with a higher sugar content and a harder rind, and ripen earlier. Although the pathogen is considered not to be seedborne, the transmission from seeds to seedlings of sweet orange has been reported [55].
3. Coffee (*Coffea arabica*): causes Coffee Leaf Scorch (CLS). The first symptoms appear on young shoots as large, scorched areas on the top or at the margins of mature leaves. The dwarf growth of new shoots, small, pale green to yellow leaves, shoot dieback, and overall plant stunting occurs. Fruit size and yield are impaired. The symptoms are severe under water stress conditions, but the trees generally do not die or only after some years [56].
4. *Prunus* spp. (peaches, almonds, and plums): in peaches, causes Phony Peach Disease (PPD). In almonds and plums, it causes leaf scorch diseases: Almond Leaf Scorch (ALS) in *P. amygdalus* and Plum Leaf Scald (PLS) in *P. domestica.* The main symptoms of PPD include stunted young shoots, more numerous and darker green leaves, early blooming, and both leaves and flowers remain on the shoots longer than expected. There are shortened twig internodes and increased lateral branching, along with severely impaired fruit production, with smaller fruits and earlier ripening.

The subspecies of *X. fastidiosa* that have been described are as follows: *X. fastidiosa* subsp. *fastidiosa*, *X. fastidiosa* subsp. *multiplex*, *X. fastidiosa* subsp. *pauca*, *X. fastidiosa* subsp. *sandyi*, and *X. fastidiosa* subsp. *tashke*. Several sources of resistance to *X. fastidiosa* have been reported in *Prunus*. Dalbó et al. [57] reported the first plum commercial cultivar resistant to *X. fastidiosa*, which apparently blocks bacterial transmission by insect vectors (sharpshooters) through a repellence effect. However, the plant is still a host to the pathogen, and it can be transmitted through other ways, such as grafting. Ledbetter et al. [58] reported that wild almonds (*P. webbii*) can be of utility in almond breeding to improve the resistance to *X. fastidiosa* infections. In other cases, Krugner et al. [59] reported that 'Nemaguard' rootstock exhibits the resistance to *X. fastidiosa*, which was unintentionally obtained while providing resistance to nematodes during the breeding process.

4.1.6. American Brown Rot Caused by *Monilinia fructicola*

This pathogen is identified in the plant as blossom blight followed by fruit rot decay, and there is a latent infection between these two phases. In blossom blight, there is a necrosis of the anthers and browning of the filaments that proceeds to the floral tube, ovary, and peduncle. Infections may extend into the twig, which may be girdled. As infected flowers wilt and turn brown, they generally firmly stick to the twig in a gummy mass. In wet weather, infected flowers become covered with greyish to tan sporodochia. additionally, apothecia (sexual fruiting structures) usually occur at the blooming time in peach trees.

Regarding the fruit rot, brown rot typically develops on mature or ripening fruits as a rapidly spreading, firm, brown decay. Under optimum conditions, the decay of ripe peaches may be visible within 48 h of infection. In advanced stages, the fruits are mummified [26] (Figure 1D).

The pathogen overwinters in fruit mummies either on the tree or the ground. In spring, asexual conidia from mummies and sexual ascospores from apothecia on the ground are the primary inoculum. These spores are wind-dispersed and germinate within 6–12 h at 15–20 °C. After 3–5 days, the blossoms become blighted and remain attached, while the infection spreads into the peduncle and down into the twig. The infection continues developing a twig canker that often develops a gumdrop as a host response. Conidia from infected tissue become a secondary inoculum to infect fruit [26].

The key to managing American brown rot is using well-timed treatments of protective fungicides with local systemic activity. The timing of the fungicide application is more critical for blossom blight control than at fruit ripening. Possible fungicide options include sterol inhibitors and succinate dehydrogenase inhibitors. However, it is fundamental to apply fungicide resistance management practices [26,60].

It is necessary to procure and to establish cultivars that exhibit epidermis-based resistance, with thicker cuticles and more waxes, pectin, phenolics, and chlorophyll. Additionally, it is important to include practices in the integrated control plan of this disease: remove mummified fruit, as well as twigs with cankers, before blooming, as well as removing alternative hosts such as wild *Prunus* species. An effective insect management is fundamental, since pests cause injuries that the fungus can penetrate through and can be important vectors during fruit ripening, carrying conidia to injuries. Thinning fruit to reduce fruit clustering, as well as removing thinned fruits from the ground, is important. Additionally, harvesting fruit at the correct maturity and avoiding wounding or bruising during harvesting is important. On the other hand, the fertilization plan must avoid the excessive application of ammonium nitrate. Finally, the use of alternative products such as calcium, vapor of acetic acid (thymol), and/or antagonistic microorganisms is recommended.

4.2. Abiotic Stresses

As mentioned, the use of rootstocks in stone fruit production includes a stronger resistance against pathogens and higher tolerance to abiotic stresses such as waterlogging, salinity, and alkalinity, among others. There is an extensive genetic diversity within *Prunus*, which provides germplasm sources that can be used as rootstocks against these abiotic stresses [61]. However, the rapid and timely identification of ideal rootstocks for fruit crops remains a great challenge [62].

4.2.1. Waterlogging

Peach trees are poorly adapted to geographic areas with poor drainage, high water tables, and high precipitation rates. Prolonged and even short exposures (~4 days) to anaerobic soil conditions can be very damaging to the root system.

Breeding efforts for rootstocks mainly focus on peaches, although most *Prunus* rootstocks may be utilized for several stone fruit species. In traditional dry land almond production, almond seedlings are used as rootstocks because of their deep growth and associated efficiency for nutrient and water uptake [63]. However, almond and peach × almond hybrid rootstocks are not suitable for wet, heavy, and inadequately drained soils but can adapt to permeable soils with medium or high fertility [64]. The deeper almond-type tap roots are more susceptible to asphyxiation and disease in even occasionally saturated soils. The intensity of the waterlogging effect is more pronounced if the plant is actively growing as compared to dormant trees [65]. Shallower rooted peach and plum rootstocks currently used for peaches have often been more effective for almonds in saturated soils. In irrigated soils, the proliferation of near-surface roots often suppresses deeper taproot formation, even in rootstock showing such growth under dryland production [66].

An increased tolerance to heavy soils and water-saturated soils is becoming an important goal for new hybrids [67]. The differences in waterlogging tolerance found among *Prunus* species other than peaches are based on complex anatomical processes such as aerenchyma formation and biochemical adaptation involving the fermentative pathways to obtain energy. Various plum and interspecific hybrids have been reported to be tolerant to waterlogged soils [20]. Several candidate genes have been identified to be involved in the tolerance in *Prunus* genotypes [65]. Other advances have been made in developing waterlogged and compact soil-tolerant plum-based rootstocks that are graft-compatible with peaches [66]. Many European *Prunus* rootstocks developed in the last decades have been listed as tolerant to waterlogging. Many of these rootstocks were developed in Mediterranean climates that receive their rainfall in the winter. However, in other peach-growing areas of the world, such as Eastern North America, waterlogging can occur during the spring and summer growing seasons. Therefore, in regions outside where these rootstocks were developed, it is uncertain whether these rootstocks are tolerant to wet soil conditions in both the dormant and the growing seasons. Additional testing will be needed to answer these questions [20].

Plum rootstocks are the most tolerant to water-logged conditions. Unfortunately, due to graft incompatibility and the effected fruit sizes, these cannot be recommended for commercial peach production. However, there is a limited level of tolerance to this condition among peach and peach × almond rootstocks. For this reason, it is recommended not to plant in areas where there are potential problems with soil waterlogging and under no circumstances to use peach × almond rootstocks in periodically waterlogged soils. Unfortunately, this is not an option in South-central Florida, where a large proportion of the available soils for peach production are spodosols [68].

4.2.2. Alkalinity

Alkaline soils are those soils having a soil solution pH above neutrality (pH > 7). High pH soils cover more than 30% of the Earth's surface [69]. Their concentration of free $CaCO_3$ in the upper horizon varies from a few percent to 95%. The higher the alkalinity, the greater the challenge in terms of adequate mineral nutrition. These soils pose challenges for the plant regarding the low availability and uptake of P, Zn, Fe, Mn, Cu, and B. The rate of boron and phosphate uptake decreases when the pH of the external solution is increased. The solubility of Fe is extremely low in aerated alkaline soils. Similar to Fe, Zn deficiency is most prevalent in alkaline soils [70].

In general, arid and semi-arid soils are alkaline and most often calcareous in nature. These soils can often be confused with those characterized as calcareous, sodic, or even saline soils, even though most of these soils are also alkaline. For instance, calcareous soils contain high concentrations of free $CaCO_3$ and other carbonates, such as dolomite. Sodic soils are often alkaline, but the degree of alkalinity can vary depending on the mineralogy and accompanying anion. Some sodic soils are dominated by chloride, sulfate, and bicarbonate. A "saline–alkali soil" has a combination of harmful quantities of salts and either a high alkalinity or high content of exchangeable sodium or both, as distributed in the profile [71].

In alkaline soils, a high pH, lime, and active lime contents cause iron chlorosis in peaches. This is evidenced in lower levels of chlorophylls, total Fe, and active Fe contents in the leaves of trees grown on soils with a high pH and active lime content [72]. The peach × almond hybrids are primarily used in calcareous soils, since they tolerate iron chlorosis well and are graft-compatible with peaches. They are also vigorous and, therefore, appropriate for use in poor, dry soils and fruit tree replanting situations [73]. Presently, peach × almond hybrid rootstocks are commonly used in calcareous soils to ensure sufficient iron uptake by the plant [20].

The peach × almond rootstocks perform better than peach rootstocks under alkaline soil conditions, because peach is particularly susceptible to alkalinity, whereas peaches × almonds are tolerant interspecific hybrids, which is a trait originating from almonds [25,73]. Despite peaches and almonds belonging to the same subgenus, these species have contrastingly different performances under alkalinity. Peaches evolved in the Eastern regions of China, in a more humid climate and at lower elevations, with more temperate climates [74], whereas almonds evolved in Western Asia in arid steppes, deserts, and mountainous areas, under severe conditions adapted to resist drought and calcareous soils and to develop a deeper and extensive root system [75]. There are several peach × almond rootstocks suitable for alkaline soils, such as 'GF-677', 'Hansen 2168', 'Hansen 536', 'Adafuel', 'Castore', 'Felinem', 'Garnem', 'Monegro', 'Polluce', and 'Adarcias', among others [1]. The better performance of peach × almond hybrids in alkaline soils is due to their tolerance to iron chlorosis, a nutritional disorder also known as lime-induced chlorosis, caused by iron (Fe) immobilization due to the high pH (7.4–8.5) and high level of bicarbonate (20%) of alkaline soils [20,72].

In order to uptake Fe^{+2} ions, *Prunus* uses a redox mechanism response that is confined to the apical zones of growing roots [76]. The response mechanism is based on the acidification of the rhizosphere by a proton pump (H^+-ATPase) that increases the solubility of Fe^{+3} complexes. This is followed by the reduction of Fe^{+3} by ferric chelate reductases (ferric reduction oxidase enzymes, such as FRO_2). Subsequently, the Fe^{+2} ions are transported through the plasma membrane of the root epidermis cells by iron-regulated transporter 1 (IRT1) [77].

According to the above-mentioned, the improved performance of peach × almond rootstocks in alkaline soils corresponds precisely to a better performed strategy. This was confirmed by Cinelli et al. [78] and Guardia et al. [79], who studied the root-associated Fe^{+3} reductase activity and iron absorption to determine the physiological traits that cause the rootstock tolerance to iron chlorosis under alkaline soil conditions. In Cinelli et al.'s study [78], the peach × almond hybrids exhibited a much higher increase in their capacity to reduce Fe^{+3} as its physiological response to stress conditions by increasing their Fe reduction capacity and the iron uptake enormously. The ferric chelate reduction capacity is restricted to the root epidermis, including the root hairs. Therefore, the inhibition of new growth or the death of younger roots could reduce the acidification of the medium, iron reduction, and iron uptake by iron-deficient plant roots [80]. Longnecker and Welch [81] hypothesized that resistance to chlorosis is correlated to the capacity of the different genotypes to accumulate a large pool of root iron, since this root accumulation is apoplastic. Through this means, iron would precipitate on the surface of roots or within the roots, apparently making the root system the major iron accumulation site. Finally, the short-term accumulation of iron reserves in roots could be followed by the translocation of large quantities of the element towards the shoots.

4.2.3. Salinity

In the last decades, increasing shifts in the climatic patterns and the expansion of farming activities have gradually increased in groundwater salinity and soil salinization, with adverse effects on peach growth and development [82]. Salinity refers to the total concentration of the major dissolved inorganic ions Na^+, Ca^{+2}, Mg^{+2}, K^+, HCO^{-3}, ${SO_4}^{-2}$, and Cl^- in the soil solution [83]. High salt levels lead to osmotic stress coupled with ionic imbalances [83]. Salinity stress significantly diminishes the vegetative and physiological characteristics and yields in stone fruit trees [84]. The severity of its effects varies among rootstocks [85], and the role of the rootstock is crucial in determining the tree performance under saline conditions [86]. Rootstock cultivars, such as 'Garnem' ('Garfi' Almond × 'Nemared'), have been widely used in several Mediterranean countries for almonds and peaches because of their deep root system and tolerance to drought [87].

Salinity affects photosynthesis by reducing the pigment concentration by changing the chloroplast ultrastructure [88]. Stomatal conductance and plant respiration are inhibited by altering the plant's water status. Additionally, NaCl toxicity is induced when toxic concentrations of chloride are accumulated in tissues. Excessive amounts of NaCl in the soil may cause the stunting or death of peach seedlings. The growth and development of plants, such as peach trees, is limited, and physiological and metabolic disorders arise as the membrane permeability increases.

Prunus hybrids such as GF-677, a peach × almond hybrid, or almond rootstocks present a degree of osmotic adjustment under salinity conditions (high NaCl concentrations) but use different osmolytes to achieve it [89]. It has been found that some cultivars of plums are highly tolerant to salinity due to a reduced absorption of salt in the roots. In contrast to the above-mentioned plums, 'Nemared' peaches are one of the most sensitive. By grafting scions onto these rootstocks, the degree of tolerance of the rootstock is conferred on the scion cultivar [90].

5. Advantages and Disadvantages of Commercial Rootstocks for Peaches

There has been remarkable progress in the development of new rootstocks for stone fruits. Interspecific hybrids between different *Prunus* species confer traits that *P. persica* lacks, such as growing in nonoptimal and low-chill areas, adaptation or tolerance to heavy soils, waterlogging, alkalinity, drought, reduced vigor for higher planting densities, and soil pathogens, among others [25], with a broad graft compatibility within *Prunus* [5,24].

Given the wide variability and contrasting differences between the cultivar traits, it is not easy to mention their features as a group of plant materials. However, it can be noticed that, in general, many peach rootstocks are more tolerant to nematodes, peach × almond hybrids are more tolerant to alkalinity and drought, and peach–plum hybrids are more tolerant to waterlogging (Table 1).

5.1. Peach Rootstocks

Peaches belong to *Euamygdalus* species cultivars, from Subgenus *Amygdalus* [91], one of the three traditionally identified rootstocks groups based on their genetic origin. In addition, it is noteworthy that open-pollinated peach seedlings are still the most widely used rootstock for peaches worldwide [20]. Actually, the only recommended rootstock for commercial peach production in Florida is 'Flordaguard' [92].

Nevertheless, other species belonging to the *Euamygdalus* section are peach (*P. persica*) wild relatives, such as *P. davidiana*, *P. kansuensis*, *P. mira*, and *P. ferganensis*, which evolved in China. The crosses of these "wild peaches" with *P. persica* have produced good quality rootstocks [93].

A wide number of different *P. persica* cultivars are used as rootstocks for peach production worldwide, making it difficult to generalize their features. Thus, the peach rootstocks advantages and disadvantages are going to be mentioned based on the most-used (>95%) *P. persica* cultivars as rootstocks for peach production in the United States, including 'Floridaguard', according to Reighard and Loreti [20]: 'Lovell', 'Halford', 'Nemaguard', 'Nemared', 'Bailey', and 'Guardian'^{TM}.

In field-testing, these rootstocks differ in vigor, root-knot nematode resistance, and bacterial canker (i.e., PTSL) tolerance but have similar effects on many other horticultural traits. These peach seedling rootstocks are susceptible to the same soil diseases and conditions, limiting their productivity and longevity in many otherwise good production sites [20].

5.1.1. 'Nemaguard'

'Nemaguard' rootstock exhibits uniform and vigorous seedlings. It imparts excellent scion vigor and productivity. Additionally, it has good resistance to *M. Incognita*, *M. Javanica*, and *M. Arenaria* [39]. However, it is sensitive to *Pratylenchus vulnus*, fungal root rots, *Verticillium*, iron chlorosis, and root waterlogging. It may reduce the winter hardiness of scion cultivars in cold climates. It produces suckers extensively. It is very sensitive to ring nematode (*M. Xenoplax*), which makes the tree more susceptible to bacterial canker and PTSL. It is fairly tolerant to crown gall [94,95].

5.1.2. 'Nemared'

'Nemared' rootstock exhibits uniform and vigorous seedlings. The seedlings have few lateral branches, which facilitates budding. It produces a slightly more vigorous tree with equal or better root-knot resistance. However, it is highly susceptible to bacterial cankers [20].

Table 1. A detailed comparison of the advantages and disadvantages of rootstocks for commercial peach production in the Southeastern United States.

Rootstocks	Cultivar	Advantages	Disadvantages	Source
Peach (*Prunus persica*)	'Nemaguard'	• May reduce cold hardiness of scion cultivars in cold climates • Uniform and vigorous seedlings • Resistant to: *Meloidogyne incognita* *M. javanica* *M. arenaria* Crown gall (relatively)	• Susceptible to: Root-lesion nematode (*Pratylenchus vulnus*) Fungal root rots *Verticillium* Ring nematode (*M. xenoplax*) • Sensitive to: Iron chlorosis Root waterlogging • Produces suckers extensively	(Handoo et al. 2004; Nyczepir et al. 1983; Zehr et al. 1976)
	'Nemared'	• Uniform and vigorous seedlings • Few lateral branches, which facilitates budding	• Highly susceptible to bacterial canker (*Pseudomonas syringae* pv. *syringae*)	(Reighard & Loreti 2008)
	'Guardian'™	• Uniform and vigorous seedlings • Excellent scion vigor and productivity • Good resistance to: *M. incognita* *M. javanica* *M. arenaria* • Tolerant to: Bacterial canker Peach Tree Short Life (PTSL) • Survives better ring nematodes in the Southeast United States	• Lower seed germination • Slightly less root-knot nematode resistance than 'Nemaguard' • Susceptible to: Oak root rot (*Desarmillaria tabescens*). Root-lesion nematode (*P. vulnus*)	(Blaauw et al. 2020)
	'Lovell'	• High seed germination • Uniform seedlings • Does not sucker • Better tolerance than 'Nemaguard' to: Ring nematodes Bacterial canker PTSL	• Scion vigor is slightly less than on 'Nemaguard' • Susceptible to: Oak root rot Root-lesion nematode *Phytophthora* spp. • Sensitive to waterlogging	(Reighard & Loreti 2008)

Table 1. *Cont.*

Rootstocks	Cultivar	Advantages	Disadvantages	Source
Peach (*Prunus persica*)	'Halford'	• High seed germination • Uniform seedlings	• Scion vigor is slightly less than on 'Nemaguard'	(Reighard & Loreti 2008)
	'Bailey'	• Uniform seedlings with good vigor • Good cold hardiness • Fair tolerant to root-lesion nematode • Produces a slightly smaller tree than 'Lovell', but is very productive • It is a popular rootstock on sandy soils in more northern climates	• Susceptible to: Root-knot nematodes Fungal root rots PTSL • No tolerant to waterlogging	(Reighard & Loreti, 2008)
	'Flordaguard'	• Low chill requirements • Red-leaved • Resistant to *M. floridensis* • Single-seeded, thus does not have to be cracked for seed separation before planting	• Not tolerant to waterlogging • Sensitive to iron deficiency chlorosis under alkaline conditions • Susceptible to peach gummosis (*Botryosphaeria dothidea*)	
Peach' almond rootstocks *P. persica´ P. dulcis*	'GF-677'	• 10–15% more vigorous than peach seedlings • Good anchorage • Lower replant problems • Adapted to infertile and droughty soils • Highly tolerant to iron chlorosis • Tolerates moderate salinity levels	• Produces high branching in the nursery • Excessive scion vigor. Induces delayed precocity, low yields, smaller fruit size, and poor fruit color in the first years • Not recommended for very fertile soils or high planting densities • Sensitive to waterlogging • Susceptible to: Oak root rot *M. incognita* *A. tumefaciens* *Phytophthora cactorum* *Stereum purpureum* • Fairly susceptible to *Verticillium alboatrum*	(Loreti & Massai 2006)

Table 1. *Cont.*

Rootstocks	Cultivar	Advantages	Disadvantages	Source
	'Sirio'	• Efficiently propagated in vitro • Adapted to fertile and permeable soils • Tolerant to iron chlorosis • Induces trees about 40% smaller than 'GF-677', with an earlier yield • Larger fruit size and improved fruit color • Suitable for high-density planting systems	• Poor root induction ability • Difficult to propagate by cuttings and layering	
	'Castore'	• Can be propagated in vitro • Semi-dwarfing • Induces higher Soluble Solid Content (SSC), favorable sugar:acid ratio, and intense fruit color • Very suitable for fertile soils and high-density planting systems	• Poor root induction ability • Unsuitable for heavy and waterlogged soils	
Peach' almond rootstocks *P. persica'* *P. dulcis*	'Polluce'	• Can be propagated in vitro • Semi-dwarfing • Adapted to permeable soils with medium to high fertility • Induces about 20% less vigor than 'GF-677', • Induces good yields with high yield efficiency and improved fruit quality	• Poor root induction ability • Unsuitable for wet, heavy, and inadequately drained soils	
	'Hansen 2168' 'Hansen 536'	• Tolerant to drought and saline soils. • Can be micropropagated in vitro. • Resistant to root-knot nematodes: *M. incognita* *M. javanica* • Moderately tolerant of *Phytophthora* spp.	• Very sensitive to crown gall and *Verticillium* wilt • Not tolerant to waterlogging nor calcareous soils as 'GF 677'	(Reighard & Loreti 2008)

Table 1. *Cont.*

Rootstocks	Cultivar	Advantages	Disadvantages	Source
Peach′ almond rootstocks *P. persica* ´ *P. dulcis*	‘Adafuel’	• Propagates easily by hardwood cuttings • Suitable for calcareous and well-drained loam soils • Resistant to: Powdery mildew (*Sphaerotheca pannosa*) Plum rust (*Tranzschelia pruni-spinosae*) Shot hole (*Corineum beijerinckii*) *Phytophthora* spp. • More tolerant to chlorosis than the ‘GF-677’. • Does not seem as sensitive to *Agrobacterium* spp. as ‘GF-677’	• Extremely vigorous • Very susceptible to *Meloidoigyne* spp.	(Reighard & Loreti 2008)
	‘Adarcias’	• Propagates readily by hardwood cuttings • Can be micropropagated in vitro • Induces lower vigor than ‘Adafuel’ and ‘GF-677’ • Induces higher fruit soluble solids content (SSC) • Resistant to: *Colletotrichum beijerinckii* Oud. *T. pruni-spinosae* (Pers.) Diet.		(Albás et al. 2004)
	‘Felinem’ ‘Garnem’ ‘Monegro’	• Propagate well by hardwood and softwood cuttings as well as in vitro • Facilitate the nursery operations by: Long vegetative period Red-colored leaves Low presence of feathers • As or more tolerant to ferric chlorosis as ‘GF-677’ • Adapt well to poor soils that are well-drained • Very resistant to: *M. incognita* *M. javanica*	• Sensitive to waterlogging • Susceptible to: Root-lesion nematode (*P. vulnus*) Crown gall caused by *Agrobacterium tumefaciens*	

Table 1. *Cont.*

Rootstocks	Cultivar	Advantages	Disadvantages	Source
Peach ´ plum rootstocks *P. persica ´* *P. cerasifera*	'Ishtara'	• Non-suckering • Semi-dwarfing rootstock (Reduces tree size 15–20%) • Induces a high productivity index and increased fruit size • Can be propagated readily by hardwood or semi-hardwood cuttings • More tolerant to *Armillaria mellea* than peach • Resistant to root-knot nematodes	• Sensitive to winter waterlogging	
	'Myran'	• More resistant than peach and peach × almond to *A. mellea* • Tolerant to: *M. arenaria* *M. javanica* *M. incognita* • Tolerant to alkaline soils (ph~8) • More tolerant to root anoxia than peach and peach × almond hybrids • Lightly more vigorous than peach seedlings	• Susceptible to *P. vulnus*	
	'MP-29'	• Shows red leaves, which simplifies the identification and removal of rootstock suckers. • Resistant to: PTSL *M. incognita* *M. floridensis* • Readily propagated via softwood or hardwood cuttings and tissue culture. • Induces significantly lower vigor than peach seedling rootstocks • Produces fewer root suckers than 'Guardian'TM • Yield efficiency is equal to or better than trees on 'Guardian'TM	• Significantly more resistant to *A. tabescens* root rot than 'Sharpe' or 'Guardian'^{TM}	(Beckman et al. 2012)

Table 1. *Cont.*

Rootstocks	Cultivar	Advantages	Disadvantages	Source
Peach ´ plum rootstocks *P. persica* ´ *P. cerasifera*	'Controller 5'	• Reduces vigor 50–60% compared to 'Nemaguard'	• Less resistant to root-knot nematodes than 'Nemaguard'	
	'Controller 9'	• Reduces vigor ~90% compared to 'Nemaguard'	• Less resistant to root-knot nematodes than 'Nemaguard'	
	'Krymsk 86'	• Non-suckering • Easily propagated by softwood and hardwood cuttings • Tolerant to calcareous soils • Induces more cold tolerance and precocity than peach rootstocks • More tolerant to waterlogging than peach seedling rootstocks		
	'Sharpe'	• Semi-dwarfing performance • Compatible with peach, nectarine, and plum cultivars • Resistant to: *Armillaria* root rot (*Desarmillaria tabescens*) PTSL *M. floridensis*	• Not recommended for commercial production but for backyard orchards since it induces smaller fruit	

5.1.3. 'Guardian'^{TM}

'Guardian' rootstock exhibits uniform and vigorous seedlings. It imparts excellent scion vigor and productivity. It has good resistance to *M. incognita*, *M. javanica*, and *M. arenaria*. It has a higher tolerance to ring nematode, bacterial canker, and PTSL. It survives better than other commercial peach rootstocks, including 'Lovell', on sandy, replant sites infested with ring nematodes (*M. xenoplax*) in the southeast [96]. Among its disadvantages, it has lower seed germination and has slightly less root-knot nematode resistance than 'Nemaguard' [97–100]. Additionally, it is susceptible to oak root rot and to *P. vulnus* (root-lesion nematode) [96].

5.1.4. 'Lovell' and 'Halford'

'Lovell' and 'Halford' rootstocks present high seed germination and uniform seedlings. 'Lovell' does not produce suckers and has a better tolerance to ring nematodes, bacterial canker, and PTSL than 'Nemaguard'. However, its scion vigor is slightly less than 'Nemaguard'. 'Lovell' is susceptible to root-knot and root-lesion nematodes, as well as crown gall, *P. vulnus, Phytophthora* spp., and *Armillaria* spp. Additionally, 'Lovell' is susceptible to waterlogging. 'Lovell' rootstock is no longer used as a commercial cultivar [20].

5.1.5. 'Bailey'

'Bailey' rootstock exhibits uniform seedlings with good vigor. It has good cold hardiness for a peach and is fairly tolerant to root-lesion nematodes. Usually, 'Bailey' produces a slightly smaller tree than 'Lovell' but is very productive. It is a popular rootstock on sandy soils in more northern climates. However, 'Bailey' is susceptible to root-knot nematodes, waterlogging, fungal root rots, and PTSL in the Southern United States [20].

5.1.6. 'Flordaguard'

Peach seedlings generally show susceptibility to root-knot nematodes, but 'Nemaguard' and 'Okinawa' showed tolerance to a nematode attack [101]. These two materials with 'Nemared' have been the most used rootstocks in Florida for years. However, they are not tolerant to root-knot *M. floridensis* found in Florida soils. 'Flordaguard' rootstock was released as a solution to this challenge. 'Flordaguard' is a low-chill, nematode-resistant peach rootstock developed for Florida soils, where *M. floridensis* is found. This rootstock has improved root-knot nematode resistance and is red-leaved, which allows for the easy detection and removal of rootstock suckers [102]. Additionally, it is single-seeded and, thus, does not have to be cracked for seed separation before planting [19]. It was released by the University of Florida in 1991 and is currently the predominant rootstock in orchards throughout the state [19]. However, this rootstock is not tolerant to waterlogging, which is a common problem in Florida flatwoods [103]. However, it is susceptibility to iron deficiency chlorosis under alkaline conditions [104], with a. susceptibility to bark gummosis, produced by *B. dothidea* [105].

5.2. Peach × Almond Rootstocks

5.2.1. 'GF-677'

'GF-677' rootstock is 10–15% more vigorous than peach seedlings, with a well-developed root system that ensures good anchorage and lower planting problems. It was adapted to infertile and droughty soils if they are permeable and well-drained. It is highly tolerant to iron chlorosis (good productivity even in soils with 10–12% limestone). It tolerates moderate salinity levels. It has become the most widespread rootstock in the peach-growing areas in Europe, mainly the Mediterranean Basin [106]. However, among its disadvantages, it produces high branching in the nursery and does not perform well in replant conditions [106]. It induces low yields, smaller fruit sizes, and poor fruit color in the first few years because of its excessive scion vigor [20]. It is not recommended for very fertile soils or high planting densities; it is sensitive to root waterlogging, and it is susceptible to *A. mellea*, *M. incognita*, *A. tumefaciens*, *Phytophthora cactorum*, and *Stereum purpureum.* Additionally, it is fairly susceptible to *V. alboatrum* [64].

5.2.2. 'Sirio'

'Sirio' rootstock can be propagated by cuttings and, even more efficiently, with in vitro micropropagation. It produces a good root system and is adapted to fertile and permeable soils. It is resistant to iron chlorosis. It induces trees about 40% smaller than 'GF77', with an earlier yield. The 'Sirio' rootstock has a better crop efficiency than 'GF77', with larger fruit sizes and improved fruit color. It is suitable for high-density planting systems on fertile and chlorosis-inducing soils [107]. However, it exhibits poor root induction ability and is difficult to propagate by cuttings and layering.

5.2.3. 'Castore'

'Castore' rootstocks can be micropropagated in vitro. It is semi-dwarfing rootstock, reducing the vegetative growth to about 30% less than 'GF-677'. It induces a higher SSC, favorable sugar:acid ratio, and intense fruit color. 'Castore' is very suitable for fertile soils and high-density planting systems [64]. However, it has a poor root induction ability and is unsuitable for non-tiled heavy and waterlogged soils.

5.2.4. 'Polluce'

'Polluce' is a semi-dwarfing rootstock that can be micropropagated in vitro. It is adapted to permeable soils with medium to high fertility, making this an alternative to 'GF-677' in medium- to high-fertility soils. It induces about 20% less vigor than 'GF-677', which allows closer tree spacing in orchards and easier tree maintenance. It produces good yields with a high yield efficiency and improved fruit quality [64]. However, similar to 'Castore', it has a poor root induction ability and is not suitable for wet, heavy, and inadequately drained soils.

5.2.5. 'Hansen 2168' and 'Hansen 536'

These rootstocks are tolerant to drought and saline soils. Additionally, they can be micropropagated in vitro. Both are resistant to root-knot nematodes (*M. incognita* and *M. javanica*), and 'Hansen 2168' is moderately tolerant of *Phytophthora* spp. However, among their disadvantages, they are very sensitive to crown gall and *Verticillium* wilt. Additionally, they are not tolerant to waterlogging or calcareous soils such as 'GF 677' [20].

5.2.6. 'Adafuel'

'Adafuel' rootstock is propagated easily by hardwood cuttings, with a better rooting percentage than 'GF-677'. It is suitable for calcareous and loam soils, provided they are well-drained. It is resistant to powdery mildew (*Sphaerotheca pannosa*), plum rust (*Tranzschelia pruni-spinosae*), and shot hole (*Corineum beijerinckii*). It is more resistant to chlorosis than 'GF-677'. It is resistant to *Phytophthora* spp. and does not seem as sensitive to *Agrobacterium* spp. such as 'GF-677' [106]. However, it is extremely vigorous and very susceptible to *Meloidoigyne* spp., limiting its commercial utility [20].

5.2.7. 'Adarcias'

'Adarcias' rootstock propagates readily by hardwood cuttings and can be micropropagated in vitro [108]. It induces a lower vigor than 'Adafuel' and 'GF-677' but has a greater crop efficiency [109], which reduces the tree growth and management costs. It induces a higher fruit soluble solids content (SSC). It is resistant to *C. beijerinckii* and *T. pruni-spinosae*.

5.2.8. 'Felinem', 'Garnem', and 'Monegro'

The nursery operations for these rootstocks are facilitated by their long vegetative period, red-colored leaves, and the low presence of feathers [73]. Additionally, they are as, or more, tolerant to ferric chlorosis than 'GF-677'. They adapt well to poor soils that are well-drained [73]. They are very resistant to the main root-knot nematode species (*M. incognita* and *M. javanica*) [47,110]. They are propagated well by hardwood and softwood cuttings, as well as in vitro. However, among their disadvantages, they are sensitive to waterlogging. Additionally, they are susceptible to the root-lesion nematode *P. vulnus* [111] and to crown gall caused by *A. tumefaciens*.

In general, peach × almond hybrids are very promising materials, mainly for areas where iron chlorosis constitutes a serious limiting factor [20]. Peach × almond hybrids have been showing great success in coping with calcareous soils for peach production [61].

5.3. Peach × Plum Rootstocks

5.3.1. 'Ishtara'

'Ishtara' is a non-suckering and semi-dwarfing rootstock that reduces the tree size. It induces a high productivity index and increased fruit size. It can be propagated readily by hardwood or semi-hardwood cuttings. It is more tolerant to *A. mellea* than peaches, and it is resistant to root-knot nematodes [112]. However, it is sensitive to winter waterlogging and induces weak anchorage in such conditions.

5.3.2. 'Myran'

This rootstock is more resistant than peaches and peaches × almonds to *A. mellea*. It is tolerant to *M. arenaria*, *M. javanica*, and *M. incognita*. It is tolerant to alkaline soils (pH~8). It is more tolerant to root anoxia than peaches and peach × almond hybrids [112]. However, this rootstock is lightly more vigorous than peach seedlings and is susceptible to *P. vulnus*.

5.3.3. 'MP-29'

'MP-29' rootstock shows red leaves, such as 'Flordaguard', which simplifies the identification and removal of rootstock suckers and resistance to PTSL such as 'Guardian'™ and resistance to root-knot nematodes, including *M. incognita* and *M. floridensis*. It induces a similar vigor to that of 'Sharpe' rootstock but with higher yields of larger fruits, which increases the yield efficiency. It is readily propagated via softwood or hardwood cuttings and tissue cultures. It induces a significantly lower vigor than trees budded on peach seedling rootstocks ca. 70% the sizes of trees on 'Guardian'™. It produces fewer root suckers than 'Guardian'™. The yield efficiency is equal to or better than the trees on 'Guardian'™. It is significantly more resistant to *A. tabescens* root rot than 'Sharpe' or 'Guardian'™ [35].

5.3.4. 'Controller 5' and 'Controller 9'

'Controller 5' reduces the vigor 50–60%, and 'Controller 9' reduces ~90% of what 'Nemaguard' induces, significantly reducing the pruning costs and use of ladders [113]. However, they are less resistant to root-knot nematodes than 'Nemaguard'.

5.3.5. 'Krymsk 86'

'Krymsk 86' is a non-suckering rootstock that can be easily propagated by softwood and hardwood cuttings. It is tolerant to calcareous soils and induces more cold tolerance and precocity than peach rootstocks. Additionally, it is more tolerant to waterlogging than peach seedling rootstocks [114].

5.3.6. 'Sharpe'

'Sharpe' is a plum hybrid rootstock of unknown origin, probably a hybrid of Chickasaw plums (*P. angustifolia*), discovered in Florida in 1974, named in honor to Dr. Ralph Sharpe. This rootstock cultivar was released by the USDA-ARS and the University of Florida. It exhibits a semi-dwarfing performance and is compatible with peach, nectarine, and plum cultivars. It is resistant to *Armillaria* root rot (*A. tabescens* (syn. *Clitocybe tabescens*)) and Peach Tree Short Life (PTSL). Additionally, 'Sharpe' is one of the three commercial rootstocks resistant to *M. floridensis*, together with 'Flordaguard' and 'MP-29'. However, 'Sharpe' rootstock is not recommended for commercial production but for backyard orchards, since it induces smaller fruits [34].

6. Rootstock Propagation

Peach seedling rootstocks have been primarily used for propagation because of the availability of inexpensive seeds, ease of sexual propagation, and good compatibility with peach scion cultivars [115]. Seedling rootstocks still dominate the stone fruit industry worldwide, probably because of their lower costs and ease of propagation compared to the clonal ones [24]. However, the horticultural advantages of peach × almond hybrid and plum rootstocks for peaches led to the development of new methods of vegetative propagation, and the modern trend in stone fruit production is toward the vegetative propagation of rootstocks, which can provide a more uniform tree performance [22].

Many of the new peach rootstock cultivars that have been recently released are complex *Prunus* hybrids that must be propagated vegetatively. Hardwood and softwood cutting propagation were first established by defining the most appropriate type and concentration of auxin and the timing of propagation during the year [115].

7. Wounding and Root Induction in Peach × Almond Hybrids

Wounding allows cuttings to absorb the applied growth regulators more efficiently by exposing more cambium, whose cells divide in response to auxin treatment to produce cambial callus [116]. However, according to Moshkov et al. [117], the response of plants to wounding is extremely complex and depends on other factors, and the main ones that influence rooting induction through wounding are: ethylene biosynthesis induction, auxin induction, and anatomical changes.

Ethylene biosynthesis induction is one of the early physiological responses to wounding [116] and may induce callus and shoot/root formation [118]. In the successive phases of rooting induction, ethylene has opposite effects, being promotive during the initial stage and inhibitory afterward [119]. Several cases regarding the promotive effects of ethylene on rooting have been reported: the rooting of chrysanthemum (*Chrysanthemum marifolium*) cuttings is enhanced by adding gaseous ethylene [120], the rooting of mung bean (*Vigna radiata*) cuttings increases by the induction of endogenous ethylene from wounding [121], and the root induction in nodal segments of *Populus tremula* is promoted by ethylene [122]. It has also been reported that ethylene in small concentrations and for short durations may enhance the root formation in woody plants [116]. Nevertheless, it must be mentioned that ethylene effects have a short duration, and more prolonged exposure at higher concentrations of this growth regulator inhibits rooting. Therefore, wounding the cutting may induce ethylene biosynthesis at low enough concentrations that can enhance root induction.

Regarding auxin induction, Moshkov et al. [117] stated that wounding often leads to similar effects from hormones and synthetic growth regulator application. After wounding, the endogenous hormone levels change, and callus formation and organogenesis start [123]. Authors such as Park and Son [124] suggested that wounding promotes the translocation of endogenous hormones to the scarring tissue, causing that portion of the stem cutting to have a more suitable level of growth regulators for root induction. One of the main hormones induced by wounding are auxins, which are fundamental for root initiation. In addition, there is a synergistic relation of wounding and auxins, since it has been reported in several species that explants are not as responsive to IBA unless they are wounded, confirming the advantage of wounding to enhance the rooting induction [118]. It has been proposed that wounding initiates a chemical signal that induces changes in the metabolism of the wounded cells. Thus, wounded cells at the base of the cutting enhance their receptivity to auxin and other essential compounds to rooting [116]. Breaking down cell compartments such as vacuoles, vesicles, peroxisomes, and plastids generates products called wounding-related compounds (WRCs), which enhance rooting when auxin is applied at a low concentration. Finally, it is worth mentioning that, besides auxins, wounding induces other growth regulators such as brassinosteroids, which may have a role in cell division related to rooting, and salicylate, which may enhance rooting in combination with auxins [116].

Regarding the anatomical changes that occur after wounding, roots arise from parenchymal cells adjacent to, and between, the existing vascular tissue. Thus, growth regulators such as indole-3-acetic acid (IAA) may diffuse to the adjacent cells, promoting new vascularization and rooting. As part of the plant response to wounding and root regeneration, the cells next to the cells that die due to wounding begin to divide in a few days, and a layer of parenchyma cells forms a callus that develops into a wound periderm. Afterward, the callus cells next to the vascular cambium and phloem divide and form adventitious roots, since parenchyma cells are totipotent and can differentiate into any other cell type, such as adventitious roots. This adventitious roots induction begins when callus cells become meristematic by dedifferentiation, giving place to the development of root primordia, which grows and emerges with the formation of vascular tissue between the root primordia and the existing vascular tissue of the cutting [116].

Many factors influence the root induction and differentiation of stem cuttings, such as age and physiological status of the donor plant [125], type of cutting, training of the donor tree, the tissue nutritional status, time of cutting harvest, growth regulator treatment, and nursery management practices. Hardwood, semi-hardwood, and softwood are cutting types used for rootstock vegetative propagation at a commercial scale [126]. Severe pruning encourages the formation of vigorous branches, which enhances the stem cutting rooting potential [127]. Additionally, the growth habit of the donor trees influences the rooting induction of the cuttings, according to the canopy part where the cuttings were taken from [128].

The nutritional status and health of the donor tree influences the induction of adventitious roots. In particular, nutrients such as phosphorus (P), potassium (K), calcium (Ca), and nitrogen (N) are significantly involved in the rooting process of the cuttings [129].

The time of cuttings harvest is a fundamental factor, since cuttings do not have a high rooting potential throughout the year. There is a marked response variability of cuttings to different periods of harvesting among different cultivars. For instance, December to January is the optimal time to harvest hardwood cuttings of peach × almond hybrid 'GF 677' in the Northern Hemisphere [130]. On the other hand, semi-hardwood cuttings are suggested to be harvested during mid-July to mid-August in the Northern Hemisphere.

IBA is the most widely used auxin in *Prunus* propagation. However, good results have been obtained with naphthalene acetic acid (NAA) or mixtures of the two hormones. IBA can be applied as a powder, which is more practical to handle but less effective, or as a liquid solution (1000–3000 ppm), which requires the dipping of the cutting base for a few seconds. These concentrated solutions are generally prepared as water–alcohol solutions. Nevertheless, it is preferable to use the water-soluble IBA potassium salt (K-IBA). Use of the alcohol solution can result in the tissue dehydration and disintegration of cortical tissues, predisposing the base of the cutting to fungal and bacterial attack. In addition, etiolating the cuttings or washing the cuttings for 24 h in running water prior to IBA treatment may enhance the auxin rooting effect.

Bottom heating promotes the tissue metabolic activity of cuttings that are harvested during the winter rest period (November–January), improving the rooting and following transplanting [131]. This can be achieved by maintaining the base of the cutting's temperature at 18–20 °C for a few days, while the upper part remains cooler to maintain the bud dormancy. Another beneficial practice is the spraying of the leaves with nutrient solutions. This practice is recommended to be done at the end of each daily water-misting cycle. Treatment with boron (B), potassium (K), and manganese (Mn) was similarly found to increase the rooting by preventing early leaf senescence [132].

Tsipouridis et al. [133] reported that better rooting is achieved by positioning the cuttings vertically rather than obliquely or horizontally. Cutting lengths of 20 and 30 cm are better than 10 cm, and the 'doublesplit' wounding of cuttings increases the rooting percentage by over 29% compared with the nonwounded control. Finally, alternative rooting systems such as aeroponic systems are adequate to propagate peaches vegetatively by stem cuttings [116].

8. The Study of Root System Architecture (RSA) Traits

It is now widely accepted that root system architecture (RSA) is a fundamental component of agricultural and natural ecosystem productivity [134]. Root system architecture refers to the spatial arrangement of roots and the extent of their growth in soil and can directly influence the capacity of roots to extract soil moisture and nutrients and adapt to limited resource conditions. The measuring of root growth and architecture is necessary to understand the adaptability of plants and the complex interactions of roots [135].

Traditional selection procedures used to detect the tolerance to abiotic stresses in trees are based on field evaluations and usually require several years. Therefore, new hydroponic culture evaluation methods have also been developed to select new genotypes tolerant to limiting the growing conditions [136]. Similarly, the evaluation for tolerance to waterlogging has also been conducted in specially designed tanks where the soil is flooded, and the selection is based on the rate at which plants develop symptoms of waterlogging and root asphyxia [65]. In the case of nematodes, tests are usually carried out with plants growing in infected pots established in greenhouses. With these procedures, the rootstock evaluation of these stresses can be carried out in several months [137]. High-throughput systems based on digital imaging, followed by image analysis, are currently being developed to study root growth and architecture, including rhizotrons for soil-grown plants [135]. Finally, the interest in root phenotyping has gradually evolved from static and global traits, such as root mass or length density, to dynamic and local traits, such as growth rates or insertion angles [138].

Rhizotrons are one of the most useful tools for RSA studies. These consist in boxes, which can have different shapes (square or rectangular) and dimensions according to the studied species, with a narrow thickness. In general, the boxes are filled with a given solid media (natural soil, organic substrate, etc.) to reproduce similar field conditions. One face of the rhizotron is translucent, in a material such as glass or acrylic, to observe the plant roots and collect images for data collection. The rhizotrons are supported in a dark tray and remain reclined to make the roots attach to the glass and make the capturing of images more effective.

The use of an RSA analysis presents unique opportunities for the future of peach production, as it allows breeders and researchers to check the performance of new rootstocks before lengthy field trials. This will allow researchers to pick only the most promising rootstocks with the RSA characteristics needed for more extensive trials, allowing the breeding and selection of new rootstocks for specific areas or challenges to move forward at a more rapid pace. It will also help researchers better understand the complex interactions involving plant roots, which may contribute to other important findings as well.

9. Final Remarks

The geographical origin and the conditions for the evolution of peaches help enormously to explain the contrasting traits exhibited by this and other *Prunus* species such as almonds. *Prunus* diversification throughout time and the large number of species that make up this genus provide a diverse gene pool for rootstock breeding. These characteristics have helped peach producers to overcome the different biotic and abiotic challenges that the industry faces under diverse environments. The large number and diverse cultivars of rootstock available to growers today allows peach production in areas where this was not previously possible, such as new rootstock cultivars that can resist pests and diseases under unfavorable edaphic conditions with lower environmental impacts.

In summary, there is not a “one fits all” rootstock adapted to every environment and resistant to all challenges, but we can count on a significant pool of germplasms that can be improved to meet new and developing production problems. With the growing pool of rootstocks adapted for certain environments and tolerant to various pests and diseases, it will become increasingly easy to find and select a rootstock that can tolerate the stresses specific to a region. This growing pool of rootstocks will also continue to grow the genetic diversity of *Prunus*, which can create further opportunities in the future.

The trend to propagate rootstocks by stem cuttings is becoming more important in commercial peach production. Vegetative propagation presents unique advantages, especially in terms of orchard uniformity and seedlings' feasibility of materials such as hybrid cultivars. In addition, the study of alternative rooting systems and techniques for rootstocks propagated vegetatively deserves to be studied in further detail. Given the valuable genetic heritage of the *Prunus* genus for the development of promising rootstock cultivars, the root system architecture analysis of these materials is relevant. It is necessary to study the root system's architecture for the assertive phenotyping of peach rootstocks, which has not been as studied as the aboveground part of such perennial tree species.

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