

Feature Review

Rootstocks: Diversity, Domestication, and Impacts on Shoot Phenotypes

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Grafting is an ancient agricultural practice that joins the root system (rootstock) of one plant to the shoot (scion) of another. It is most commonly employed in woody perennial crops to indirectly manipulate scion phenotype. While recent research has focused on scions, here we investigate rootstocks, the lesser-known half of the perennial crop equation. We review natural grafting, grafting in agriculture, rootstock diversity and domestication, and developing areas of rootstock research, including molecular interactions and rootstock microbiomes. With growing interest in perennial crops as valuable components of sustainable agriculture, rootstocks provide one mechanism by which to improve and expand woody perennial cultivation in a range of environmental conditions.

Getting to the Root of the Matter

Roots anchor plants in the ground, acquire water and nutrients from the soil, serve as storage organs, and are the primary zone of contact with soil organisms. Root systems vary substantially in architecture and function, both within and between species, and they are a crucial component in coordinating plant responses to a range of abiotic and biotic stressors, including pathogens, water and nutrient shortages, and potentially toxic compounds such as salt or heavy metals (e.g., [1–4]). In perennial crops and some annuals, grafting is used to join resilient root systems (rootstocks) to shoots (scions) that produce the harvested product (e.g., fleshy or dry fruits).

The vast majority of woody perennial plant cultivation involves clonal propagation [5–7], a technique that facilitated the domestication of the earliest woody crops including olive, grape, and fig [8]. In these and many other species, grafting is an important part of the propagation process. Grafting typically joins two plant organs (root system and shoot) from different individuals that form vascular connections and survive in a unique symbiotic relationship as a genetic chimera [8]. The development of grafting around 1800 BCE facilitated a ‘second wave’ of woody perennial domestication and resulted in the wide-scale cultivation of new woody crops, including many Rosaceae (apple, pear, plum, and cherry), and the improvement of previously ungrafted, clonally propagated perennials [8,9].

In long-lived woody plants, grafting is a common means to clonally propagate desirable scions, thus side-stepping challenges traditionally associated with breeding of woody perennials, including prolonged juvenile phases and primarily outcrossing reproductive systems [5]. It is becoming increasingly apparent that the use of genetically distinct individuals as rootstocks serves to improve perennial crops, with different rootstocks conferring unique traits in both belowground and aboveground components of the plant [8]. In addition to reducing the time to

Trends

As concerns mount about food security in a changing climate, attention is refocusing on perennial crops as important components of sustainable agriculture.

In many economically important woody perennial crops (e.g., many Rosaceae, *Citrus*, and grapes), a fruit-bearing shoot (scion) is grafted to a root system (rootstock) that is genetically distinct from the scion.

Rootstocks are selected for rooting and grafting capacity, abiotic and biotic stress tolerance, and their ability to beneficially alter scion phenotypes.

Relatively little is known about the diversity of rootstocks used for any given crop, the geographic origins or current distribution of cultivated rootstocks, or their domestication.

A common scion can be grafted to segregating rootstock populations to produce a genetic map of both the traits of the rootstocks themselves and their effects on scion phenotype.

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fruit set, grafting can result in trees of shorter stature, both traits favored by early farmers. In modern agriculture, grafting has greatly increased the efficiency of perennial crop breeding by allowing root and shoot traits to be selected independently rather than requiring both sets of traits to be present in a single genetic individual. Here we explore our current state of knowledge of rootstocks, the lesser-known half of the perennial crop equation. We review natural grafting, grafting in perennial agriculture, rootstock diversity and domestication, and recent advances and future directions of rootstock research, including molecular interactions and rootstock microbiomes.

Natural Grafting

Grafting occurs in natural populations of some species, a phenomenon that may have inspired the development of grafting in agriculture and horticulture [8,10]. In nature, grafting can occur between stems or roots of the same individual or the same species or even between congeners or plants of different families [11–14]. Species that naturally graft tend to spread vegetatively and grow in dense stands, often in dry, somewhat harsh environments or those with loose soils that promote shallow, far-reaching root systems (e.g., *Acer saccharinum*, *Betula lutea*, *Pinus* spp., *Populus tremuloides*, *Pseudotsuga* spp., *Thuja* spp., *Tilia americana*, *Tsuga heterophylla*, *Ulmus americana*, and several tropical species, [13,15–18]).

Seminal research in natural grafting documents the transfer of water, nutrients, compounds, dyes, silvicides, pathogens, and even genetic material between individuals through grafts [19–21]. More recently, several studies have demonstrated the transfer of fungal and bacterial pathogens through natural graft junctions, including Dutch elm disease, oak wilt, laurel wilt, tomato wilt, and citrus variegated chlorosis [20,22–27]. Chemicals used in management or treatment (e.g., ammonium sulfamate, glyphosate, propiconazole) can also move through graft junctions [19,24,25]. Furthermore, experimental work with tobacco grafts shows the transfer of partial or whole nuclear and plastid genomes short distances across graft junctions [28–30] (see below). Similarly, naturally occurring plastid and nuclear genome transfers have been documented between the tropical tree species *Amborella trichopoda* and its epiphytes, with inter-specific cellular contact occurring at wound sites [31]. Horizontal gene transfer is also present between parasitic plants and their hosts [32], but the connection of haustoria to host plant vasculature represents a very different mechanism compared with graft junctions. These findings have exciting implications for agriculture and suggest a novel mechanism for asexual speciation under certain circumstances [15,30].

Grafting in Woody Perennial Agriculture

The phenomenon of natural grafting was coopted for use in cultivation and today is an essential part of agriculture, horticulture, and silviculture. Grafting typically employs two individuals, one or both of which are clonally propagated, depending on the desired outcome: sexually produced (seed grown) rootstock and clonal scions are often used in traditional agricultural settings but also for some industrial-scale crops (e.g., *Coffea*, *Juglans*); clonal rootstocks and sexually produced scions are typically used during the cultivar breeding and selection process; and, when uniformity is desired, both rootstock and scion are clonally produced. In more advanced grafting practices, a third individual (interstock) is sometimes used to join a rootstock and scion that may otherwise be incompatible [8].

A review of the available literature indicates that more than 70 woody perennial crop species propagated for their edible fruits are grown on rootstocks (Table 1), in addition to those species used for fodder, fiber, oil, and timber. Rootstocks are widely used for economically important perennial fruit and nut species: 20 of the 25 most-produced fruit and nut crops [33] are grafted in certain circumstances (Table 2); the remaining five crops are monocots, for which grafting is not a viable method of propagation. The value of rootstocks has become evident even for annuals

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Table 1. Grafted Perennial Crop Species and Examples of Selected Rootstock Traits

Scientific Name	Common Name	Family	Targeted Trait	Refs
<i>Actinidia deliciosa</i> (A. Chev.) C.F. Liang & A.R. Ferguson	Kiwifruit	Actinidiaceae	Scion growth, water uptake	[147,148]
<i>Adansonia digitata</i> L.	Baobab	Malvaceae	Nutrient content	[149]
<i>Anacardium occidentale</i> L.	Cashew	Anacardiaceae	Salt tolerance	[150]
<i>Annona</i> spp.	Custard apple	Annonaceae	Flood tolerance	[148,151,152]
<i>Antidesma bunius</i> (L.) Spreng.	Bignay	Phyllanthaceae	None known	[148]
<i>Artocarpus altilis</i> (Parkinson ex F.A. Zorn) Fosberg	Breadfruit	Moraceae	Dwarfing	[153]
<i>Artocarpus heterophyllus</i> Lam.	Jackfruit	Moraceae	None known	[154]
<i>Asimina triloba</i> (L.) Dunal	Pawpaw	Annonaceae	Precocity	[155]
<i>Averrhoa carambola</i> L.	Starfruit/carambola	Oxalidaceae	None known	[148,156]
<i>Camellia</i> spp.	Tea	Theaceae	None known	[157]
<i>Carica papaya</i> L.	Papaya	Caricaceae	None known	[148,158]
<i>Carissa</i> spp.	Carissa, karanda	Apocynaceae	None known	[148]
<i>Carya illinoensis</i> (Wangenh.) K. Koch	Pecan	Juglandaceae	Nematode resistance	[45,159]
<i>Casimiroa edulis</i> La Llave	White sapote	Rutaceae	None known	[148]
<i>Castanea</i> spp.	Chestnut	Fagaceae	Graft compatibility	[159–161]
<i>Ceratonia siliqua</i> L.	Carob	Fabaceae	Salt tolerance	[148,162]
<i>Chrysophyllum cainito</i> L.	Star apple	Sapotaceae	None known	[148]
<i>Citrus</i> spp.	Citrus	Rutaceae	Disease resistance	[57,163–165]
<i>Coffea arabica</i> L.	Coffee	Rubiaceae	Fruit quality, production, scion growth	[166]
<i>Corylus avellana</i> L.	Hazelnut	Betulaceae	None known	[159,167]
<i>Dimocarpus longan</i> Lour.	Longan	Sapindaceae	None known	[148,168]
<i>Diospyros kaki</i> L.f.	Persimmon	Ebenaceae	Dwarfing	[148,169]
<i>Diospyros nigra</i> (J.F. Gmel.) Perrier	Black sapote	Ebenaceae	None known	[170]
<i>Durio</i> spp.	Durian	Moraceae	None known	[148,171]
<i>Eriobotrya japonica</i> (Thunb.) Lindl.	Loquat	Rosaceae	Boron and salt tolerance	[148,172]
<i>Ficus carica</i> L.	Fig	Moraceae	Disease resistance	[173]
<i>Fortunella</i> spp.	Kumquat	Rutaceae	None known	[148]
<i>Juglans regia</i> L.	Walnut	Juglandaceae	Drought tolerance	[159,174–176]
<i>Litchi chinensis</i> Sonn.	Lychee	Sapindaceae	None known	[148,177]

Table 1. (continued)

Scientific Name	Common Name	Family	Targeted Trait	Refs
Macadamia spp.	Macadamia	Proteaceae	None known	[178]
Malpighia emarginata DC	Barbados Cherry	Malpighiaceae	None known	[148]
Malus domestica Borkh.	Apple	Rosaceae	Mineral uptake, scion growth	[60]
Mangifera indica L.	Mango	Anacardiaceae	Root microbe interactions	[179]
Manilkara zapota (L.) P. Royen	Sapodilla	Sapotaceae	Dwarfing, precocity	[148,180]
Melicoccus bijugatus Jacq.	Mamoncillo	Sapotaceae	None known	[148]
Mespilus germanica L.	Medlar	Rosaceae	Fruit yield, quality	[181]
Morus alba L.	Mulberry	Moraceae	None known	[182]
Nephelium lappaceum L.	Rambutan	Sapindaceae	Rootstock growth	[148,183]
Nephelium mutabile Blume	Pulasan	Sapindaceae	None known	[148]
Olea europaea L.	Olive	Oleaceae	Drought tolerance, dwarfing	[184–186]
Opuntia ficus-indica (L.) Mill.	Opuntia	Cactaceae	Graft compatibility	[187]
Passiflora edulis Sims	Passionfruit	Passifloraceae	None known	[148]
Persea americana Mill.	Avocado	Lauraceae	Disease resistance	[158,188,189]
Pistacia vera L.	Pistachio	Anacardiaceae	Drought tolerance	[45,190,191]
Plinia cauliflora (Mart.) Kausel	Jaboticaba	Myrtaceae	None known	[192]
Pouteria spp.	Canistel, mamey sapote	Sapotaceae	Dwarfing, precocity	[148,180]
Prunus armeniaca	Apricot	Rosaceae	Fruit yield and quality	[193,194]
Prunus domestica L.	Plum	Rosaceae	Fruit quality	[195,196]
Prunus dulcis (Mill.) D.A. Webb	Almond	Rosaceae	Drought tolerance	[45,197,198]
Prunus persica (L.) Batsch	Peach	Rosaceae	Dwarfing	[148,199]
Prunus avium (L.) L., Prunus cerasus L.	Cherry	Rosaceae	Fruit size, quality, and yield, scion vigor	[58]
Psidium guajava L.	Guava	Myrtaceae	None known	[148,200,201]
Punica granatum L.	Pomegranate	Lythraceae	Fruit quality, yield, scion vigor	[202]
Pyrus communis L.	Pear	Rosaceae	Fruit yield and production, heat tolerance	[203–205]
Quararibea cordata (Bonpl.) Vischer	Chupa-chupa	Bombacaceae	None known	[148]
Sandoricum koetjape (Burm.f.) Merr.	Santol	Meliaceae	None known	[148]
Sclerocarya birrea (A. Rich.) Hochst.	Marula	Anacardiaceae	Fruit production, rootstock growth	[206]

Table 1. (continued)

Scientific Name	Common Name	Family	Targeted Trait	Refs
<i>Spondias dulcis</i> Parkinson	Ambarella	Anacardiaceae	None known	[148]
<i>Tamarindus indica</i> L.	Tamarind	Fabaceae	None known	[148,207]
<i>Theobroma cacao</i> L.	Cocoa	Malvaceae	Yield	[208–210]
<i>Vaccinium</i> spp.	Blueberry	Ericaceae	Precocity, scion vigor	[211]
<i>Vitis vinifera</i> L.	Grape	Vitaceae	Drought tolerance	[41,51,52,212,213]
<i>Ziziphus</i> spp.	Jujube	Rhamnaceae	None known	[148]

and several recent reviews have explored various aspects of grafting and rootstock–scion interactions (e.g., [8,34–42]).

Research into the domestication of woody perennial crops has lagged behind that of annuals due to the logistical difficulties of working with large, long-lived species that require immense amounts of time, space, and money to cultivate and maintain [5–7]. Grafting adds an additional layer of complexity to this work, as the performance of multiple scion–phenotype combinations must be evaluated over many years and, ideally, in many different environments. Until recently, rootstock research has focused on important horticultural goals such as improving scion phenotype [37,43] and identifying pest- and pathogen-resistant rootstocks [44,45]. However, advances in molecular techniques have made it possible to achieve a more intricate understanding of the processes involved in grafting and the role that rootstocks play in perennial crop domestication.

Rootstock Diversity and Domestication

Although grafting has been an important part of growing woody perennial crops for at least 2000 years, surprisingly little is known about the plant species that are used as rootstocks. It is clear that rootstocks for different crops are at different stages of domestication. In the early stages of rootstock use, rootstocks are used primarily as a means of clonal propagation of the scion and are chosen based on their availability with little selective pressure on specific traits. Instead, growers deal with undesirable traits using intensive and costly techniques such as pruning, fertilization, and pesticide application. As rootstock domestication advances, traits including productivity and disease resistance are often targeted. Rootstocks have a long history and an important role in agriculture, but many questions about rootstock diversity and domestication remain. How many genotypes and species are used as rootstocks for a given crop and how closely related are they to the scion species? What are the geographic origins, current distributions, and frequency of use of these genotypes? Are there morphological or genetic signatures of domestication in taxa used for rootstocks?

Rootstock Diversity

Despite a growing body of literature documenting the diversity and phylogeography of cultivated plants and their evolution under domestication, including woody perennials used as scions [6,46], rootstock species are rarely considered. Looking at some of the most economically important grafted plants in terms of tonnage (Table 2), some trends in rootstock diversity and domestication become apparent: (i) rootstock species are often closely related to but genetically distinct from the scion species they support; (ii) for a single crop, multiple species and their hybrid derivatives are often used to generate rootstocks, although (iii) ultimately relatively few rootstock genotypes are employed for a given crop in most contemporary agricultural systems; (iv) rootstock selection is a function of both the scion genotype with which it is grafted and the

Table 2. The Twenty Most-Produced Grafted Woody Perennial Crop Species, Rootstock Species Used for Their Cultivation, and Rootstock Traits Targeted During Selection

Common Name Primary Species Used as Scion (Family)	Rootstock Species	Method of Rootstock Propagation ^a	Primary Targets of Rootstock Selection	Estimated Global Production (Tonnes per Year) ^b	Refs
Apple <i>Malus domestica</i> Borkh. (Rosaceae)	<i>M. baccata</i> , <i>M. domestica</i> , <i>M. doumeri</i> , <i>M. halliana</i> , <i>M. hupehensis</i> , <i>M. sargentii</i> , <i>M. sieboldii</i> , <i>M. sieversii</i> , <i>M. sikkimensis</i> , <i>M. sylvestris</i> , <i>M. transitoria</i> , <i>M. toringoides</i> , <i>M. yunnanensis</i>	Clonal	Scion architecture and morphology, size control/dwarfing fruit quality, disease/pest resistance; abiotic tolerance: drought cold, soil conditions	80 822 521	[214–219]
Grape <i>Vitis vinifera</i> L. (Vitaceae)	<i>V. aestivalis</i> , <i>V. berlandieri</i> , <i>V. californica</i> , <i>V. labrusca</i> , <i>V. rotundifolia</i> , <i>V. rupestris</i> , <i>V. vinifera</i> , <i>V. vulpina</i>	Clonal	Scion vigor, disease/pest resistance; abiotic tolerance: drought, salt, acidic soils, iron chlorosis	77 181 122	[51,52,212]
Orange <i>Citrus × aurantium</i> L. <i>C. sinensis</i> (L.) Osbeck (Rutaceae)	<i>C. × aurantium</i> , <i>C. aurantifolia</i> , <i>C. jambhiri</i> , <i>C. limon</i> , <i>C. reticulata</i> ; hybrids of: <i>C. paradisi</i> , <i>C. resnyi</i> , <i>C. sinensis</i> , <i>C. trifoliata</i> , <i>C. volkameriana</i>	Polyembryony (clonal)	Scion architecture, size control/dwarfing, fruit quality, rapid growth, polyembryony, disease/pest resistance; abiotic tolerance: drought, cold, salt, flooding	71 445 353	[163–165,220]
Mango <i>Mangifera indica</i> L. (Anacardiaceae)	<i>M. indica</i> , <i>M. casturi</i> (trials only)	Polyembryony (clonal), seed	Size control/dwarfing, graft compatibility, polyembryony; abiotic tolerance: calcareous soil, salt	43 300 070 ^c	[221–223]
Tangerine, mandarin <i>Citrus reticulata</i> Blanco (Rutaceae)	<i>C. × aurantium</i> , <i>C. aurantifolia</i> , <i>C. jambhiri</i> , <i>C. limon</i> , <i>C. reticulata</i> ; hybrids of: <i>C. paradisi</i> , <i>C. resnyi</i> , <i>C. sinensis</i> , <i>C. trifoliata</i> , <i>C. volkameriana</i>	Polyembryony (clonal)	Size control/dwarfing, rapid growth, scion architecture, polyembryony, disease/pest resistance; abiotic tolerance: cold, drought, salt, flooding,	28 678 214	[163,164,220]
Pear <i>Pyrus communis</i> L. (Rosaceae)	<i>Amelanchier</i> spp., <i>Crataegus</i> spp., <i>Cydonia oblonga</i> , <i>P. amygdaliformis</i> , <i>P. betulifolia</i> , <i>P. calleryana</i> , <i>P. caucasica</i> , <i>P. communis</i> , <i>P. cordata</i> , <i>P. elaeagnifolia</i> , <i>P. kawakamii</i> , <i>P. nivalis</i> , <i>P. pashia</i> , <i>P. pyrifolia</i> , <i>P. syriaca</i> , <i>P. ussuriensis</i> , <i>P. xerophila</i> , <i>Sorbus</i> spp.; hybrids of: <i>C. oblonga</i> , <i>P. bretschneideri</i> , <i>P. elaeagnifolia</i> , <i>P. heterophylla</i> , <i>P. longipes</i> , <i>P. nivalis</i> , <i>P. pyrifolia</i> , <i>P. sinaica</i> , <i>P. ussuriensis</i>	Seed, clonal	Size control/dwarfing, precocity, productivity, yield, fruit quality, fruit size, ease of clonal propagation, disease resistance, graft compatibility; abiotic tolerance: cold, iron and calcium chlorosis	25 203 754	[204,205,224]
Peach <i>Prunus persica</i> (L.) Batsch (Rosaceae)	<i>P. cerasifera</i> , <i>P. davidiana</i> , <i>P. dulcis</i> , <i>P. ferganensis</i> , <i>P. insititia</i> , <i>P. kansuensis</i> , <i>P. mira</i> , <i>P. persica</i> , <i>P. pumila</i> , <i>P. salicina</i> , <i>P. spinosa</i> ; hybrids of: <i>P. angustifolia</i> , <i>P. besseyi</i> , <i>P. cerasifera</i> , <i>P. davidiana</i> , <i>P. dulcis</i> , <i>P. persica</i> , <i>P. salicina</i> , <i>P. spinosa</i>	Seed, clonal	Size control/dwarfing, ease of vegetative propagation, graft compatibility, disease/pest resistance, abiotic tolerance: drought, cold, anaerobic soil conditions, flooding, iron chlorosis, calcareous and compact soils	21 638 953	[225,226]
Olive <i>Olea europaea</i> L. (Oleaceae)	<i>O. europaea</i>	Seed, clonal	Size control/dwarfing, rooting ability, graft compatibility, disease resistance; abiotic tolerance: drought, salt	20 396 700	[185,186]
Lemon and lime <i>Citrus limon</i> (L.) Osbeck, <i>C. aurantifolia</i> (Cristm.) (Rutaceae)	<i>C. × aurantium</i> , <i>C. aurantifolia</i> , <i>C. jambhiri</i> , <i>C. limon</i> , <i>C. reticulata</i> ; hybrids of: <i>C. paradisi</i> , <i>C. resnyi</i> , <i>C.</i>	Polyembryony (clonal)	Scion architecture, size control/dwarfing, rapid growth, polyembryony, disease/pest	15 191 482	[163–165,220]

Table 2. (continued)

Common Name Primary Species Used as Scion (Family)	Rootstock Species	Method of Rootstock Propagation ^a	Primary Targets of Rootstock Selection	Estimated Global Production (Tonnes per Year) ^b	Refs
	<i>sinensis</i> , <i>C. trifoliata</i> , <i>C. volkameriana</i>		resistance; abiotic tolerance: cold, drought, salt, flooding		
Papaya <i>Carica papaya</i> L. (Caricaceae) ^c	<i>C. papaya</i>	Unknown	Fruit quality	12 420 585	[158]
Plum and sloe <i>Prunus domestica</i> L. (<i>P. spinosa</i> L. × <i>cerasifera</i> Ehrh.) (Rosaceae)	Hybrids of: <i>P. americana</i> , <i>P. armeniaca</i> , <i>P. besseyi</i> , <i>P. cerasifera</i> , <i>P. domestica</i> , <i>P. dulcis</i> , <i>P. hortulana</i> , <i>P. insititia</i> , <i>P. munsoniana</i> , <i>P. persica</i> , <i>P. pumila</i> , <i>P. salicina</i> , <i>P. spinosa</i> , <i>P. tomentosa</i>	Seed, clonal	Scion vigor and architecture, size control/dwarfing, precocity, graft compatibility, ease of clonal propagation, nutrient uptake, disease/pest resistance; abiotic tolerance: cold, calcareous soils, drought, flooding	11 528 337	[196]
Coffee <i>Coffea arabica</i> L., <i>C. canephora</i> var. <i>robusta</i> (L. Linden) A. Chev. (Rubiaceae)	<i>C. canephora</i> , <i>C. liberica</i> , <i>C. liberica</i> var. <i>dewevrei</i>	Seed	Fruit quality, growth, production, pest resistance, drought tolerance	8 920 840	[22,166,227]
Grapefruit <i>Citrus paradisi</i> Macfad. (Rutaceae)	<i>C. × aurantium</i> , <i>C. aurantifolia</i> , <i>C. jambhiri</i> , <i>C. limon</i> , <i>C. reticulata</i> ; hybrids of: <i>C. paradisi</i> , <i>C. reshni</i> , <i>C. sinensis</i> , <i>C. trifoliata</i> , <i>C. volkameriana</i>	Polyembryony (clonal)	Scion architecture, size control/dwarfing, rapid growth, polyembryony, disease/pest resistance, abiotic tolerance: cold, drought, salt, flooding	8 453 446	[163–165,220]
Tea <i>Camellia sinensis</i> L. (Theaceae)	<i>C. sinensis</i> , <i>C. irrawadiensis</i> , <i>C. taliensis</i>	Clonal	High production, drought tolerance	5 345 523	[157]
Avocado <i>Persea americana</i> Mill. (Lauraceae)	<i>P. americana</i>	Clonal, (seed)	Precocity, disease resistance, salt tolerance	4 717 102	[189]
Persimmon <i>Diospyros kaki</i> L.f. (Ebenaceae)	<i>D. rhombifolia</i> (as interstock), <i>D. virginiana</i>	Seed	Size control/dwarfing, graft compatibility	4 637 357	[169,228]
Cocoa <i>Theobroma cacao</i> L. (Malvaceae)	<i>T. cacao</i>	Clonal	Size control/dwarfing, cultivation density, disease resistance	4 585 552	[209,210]
Cashew nut <i>Anacardium occidentale</i> L. (Anacardiaceae)	<i>A. occidentale</i>	Seed	Size control/dwarfing, precocity	4 439 960	[229]
Apricot <i>Prunus armeniaca</i> L. (Rosaceae)	<i>P. armeniaca</i> , <i>P. cerasifera</i> , <i>P. domestica</i> , <i>P. mume</i> , <i>P. persica</i> , interspecific hybrids thereof	Seed, (clonal)	Scion vigor, fruit size, yield, tree longevity, precocity, rootstock vigor, graft compatibility, disease/pest resistance; abiotic tolerance: salt, cold	4 111 076	[194,230,231]
Walnut <i>Juglans regia</i> L. (Juglandaceae)	<i>J. hindsii</i> , <i>J. major</i> , <i>J. mandshurica</i> , <i>J. microcarpa</i> , <i>J. nigra</i> ; hybrids of: <i>J. nigra</i> and <i>J. hindsii</i> , <i>Pterocarya stenoptera</i>	Seed, (clonal)	Disease resistance; abiotic tolerance: salt, acidic soils	3 458 046	[175,176]

^aClonal, asexually produced; seed, sexually produced; polyembryonic, from clonal embryos.

^bData from [26].

^cEstimated tonnage for *M. indica*, *Garcinia mangostana*, and *Psidium guajava* combined.

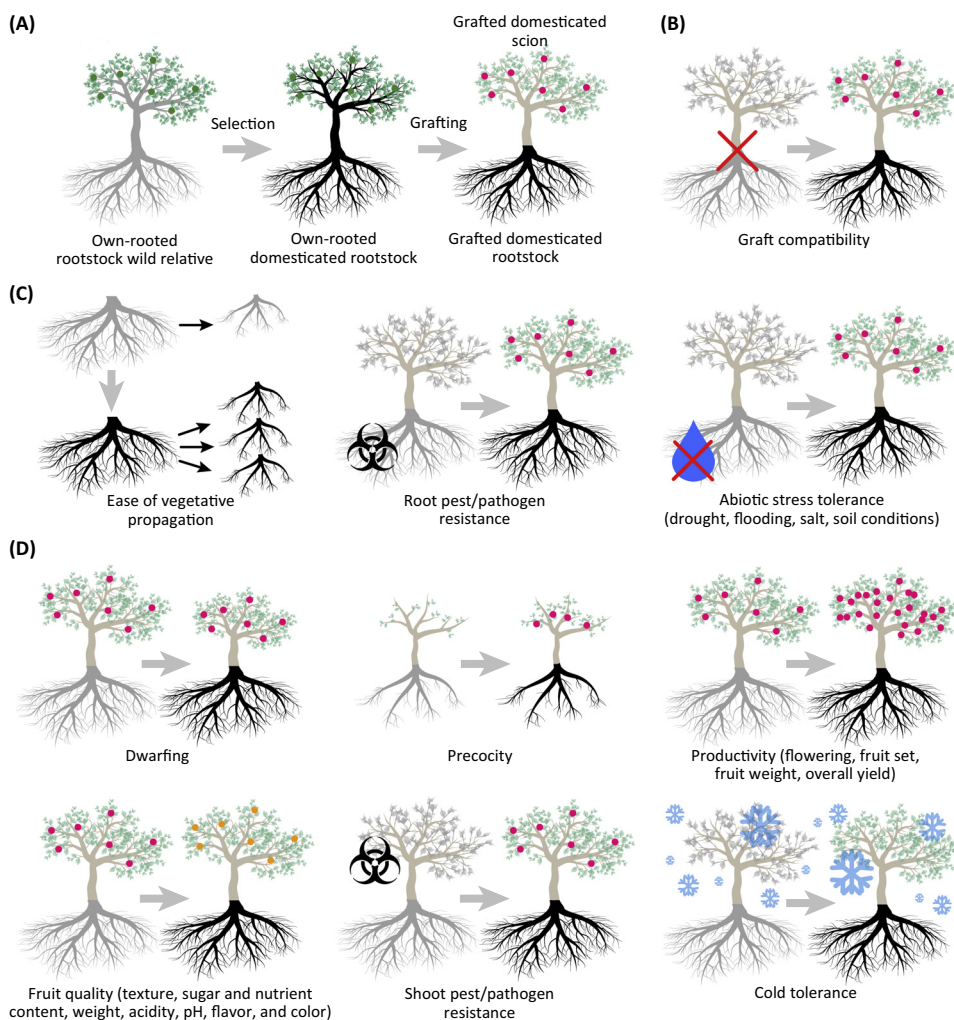
Carica papaya is an herbaceous perennial, but is included here because cultivation and production practices are similar to those of woody perennials.

environment in which the grafted plant will be grown [47]; and (v) rootstocks are selected not only for traits inherent in the root system but also for traits imparted to the scion (Figure 1, Key Figure).

For example, the introduction of the North American aphid *Phylloxera* into Europe in the mid-1800s devastated the grape (*Vitis vinifera*) industry on the European continent [48]. Grafting *V. vinifera* scions onto *Phylloxera*-resistant rootstocks allowed *V. vinifera* to grow in the presence of *Phylloxera* and today grafting is commonplace in grape, with native North American grapevine species functioning as indispensable resources for the development of abiotic and biotic stress-resistant rootstocks [49,50]. *Vitis riparia* and *Vitis rupestris* were initially selected for *Phylloxera*

Key Figure

Primary Targets of Rootstock Selection



Trends in Plant Science

Figure 1. Rootstocks used in perennial agriculture (A) have been selected from a pool of wild germplasm and bred for (B) their ability to graft to cultivated scions, (C) the root phenotype, and (D) their ability to impact the phenotype of the grafted scion.

resistance and for their capacity to self-root. Subsequent integration of *Vitis berlandieri* into rootstock development programs expanded the potential range of vineyards because of its tolerance of chalky soils like those found in the Champagne and Cognac regions [49]. Today, grapevine scions are primarily grafted on these three species and their hybrid derivatives, although other species are also used [51–53] (Table 2).

Given that graft compatibility can occur across broad phylogenetic distances, crop wild relatives are of great significance to grafted perennial crops. This underscores the importance of maintaining significant living collections of perennial crop wild relatives that represent a range of variation in morphology, phenology, and ecology [54], not only for scions but also for rootstock development. Much like in crop breeding, rootstock breeding and selection efforts often target wild and semidomesticated species, feral individuals, and landraces that are thought to be disease and stress resistant and that are adapted to local environments.

Evolution of Rootstock Species under Domestication

Rootstock species are considered to be undergoing domestication because they are part of a mutualistic relationship between humans and plants that enhances the fitness of both the domesticator and the domesticate [55]. Although rootstock breeding clearly targets specific traits (Figure 1), to our knowledge no formal description of a ‘domestication syndrome’ exists for rootstock species. Further, few comparative morphological or genetic studies of rootstocks and their wild ancestors exist to infer signatures of rootstock domestication. Many rootstocks are derived from perennial, outcrossing wild species (Table 2) and exhibit some of the hallmarks of woody plant domestication, including high levels of heterozygosity and extensive clonal propagation [5–7]. However, rootstock species are unlike most other domesticated perennials in that, while some traits under selection are directly expressed in the rootstock itself (e.g., pathogen resistance), others are expressed in the grafted scion (e.g., dwarfing) (see below).

In general, grafting affects three major processes in a plant: uptake and transport of water and nutrients, hormone production and transport, and the large-scale movement of proteins, mRNAs, and small RNAs (sRNAs). These processes have implications for both belowground and aboveground functioning, but the interconnectedness of the variables at work in rootstock–scion interactions (rootstock genotype, scion genotype, environment) obscures individual contributions to phenotypic variation. Certainly, the genotypes of both rootstock and scion play an important role in these interactions, and different combinations of stock and scion are known to vary in their phenotypic effects (e.g., [56–60]). Additional factors impacting rootstock–scion interactions include the age of the grafted individuals, the grafting technique employed, seasonality, time since grafting [15,40], genotype \times environment and genotype \times genotype \times environment interactions, root morphology and architecture [42], the degree of rootstock–scion compatibility, and root–microbe interactions. Below, we consider the primary traits targeted during rootstock selection (Figure 1) and assess our current understanding of their genetic underpinnings.

Graft Union Formation and Graft Compatibility

The development and integration of highly efficient root systems in crops through grafting is possible only if the rootstock and scion are graft compatible. Consequently, the primary selection factor for any rootstock is its ability to form the tissue that serves as the junction between the rootstock and scion: the graft union [15,34]. The healing of the graft union can take anywhere from days in the case of herbaceous plants to more than 1 year in the case of some woody perennials [40] and in some cases graft incompatibility may not become apparent for several years [61,62]. The quality of vascular connections formed in the graft union varies between rootstock–scion combinations and can impact water transport from root to shoot for long periods of time or permanently [15,34,36,40]. Work in *Arabidopsis* suggests that intertissue

communication, cell interdigitation, and auxin responses are all important for the success of graft unions [63]. Despite being the single most important factor required for grafting, the mechanisms of graft compatibility and incompatibility are still not well understood at the physiological or molecular level [15].

Root Structure and Function

Assuming a successful graft union, rootstocks are selected in part for traits inherent to the root system itself, primarily resistance to soil-borne pests and pathogens (e.g., [35]), and tolerance to abiotic stressors such as salinity, drought, and flooding [40] (Tables 1 and 2). How do processes occurring in the root impact stress response in other parts of the plant? In many ways our understanding of root structure and function has lagged behind that of easier-to-observe aboveground organs (e.g., [64,65]), but several recent reviews report that root anatomy can mediate responses to a range of abiotic and biotic stressors [3,4,66–70]. For example, shifts in key anatomic traits – from root cortical aerenchyma to xylem diameter and conductance to variation in root hairs to endo- and exodermal lignification and suberization that reduce root water loss – all have the potential to increase late-season water availability [69]. While many crops exhibit substantial variability in root anatomy, selection of improved root systems – those that are deep rooting, less metabolically active, or more water conserving – comes with costs such as less root mass to forage for soil phosphorus at shallow depths, reduced efficiency at exploiting ephemeral nutrient patches, and exposure to more challenging abiotic conditions (e.g., low temperatures, salinity, compaction, aluminum or manganese toxicity) at deeper soil levels [71]. Nonetheless, for many crops in many soils, a deep-rooting, water-conserving root phenotype is likely to have several advantages (e.g., [68]).

Rootstock Modulation of Scion Phenotypes

In addition to selecting for phenotypes expressed in the roots, rootstocks are also selected based on their effects on the scion, including precocity (early bearing), production, disease resistance, and fruit quality (Tables 1 and 2; Figure 1). One of the most sought-after phenotypes – rootstock-induced reduction in scion vigor, or ‘dwarfing’ – causes a decrease in tree volume, height, canopy diameter, and circumference [40], reducing the need for pruning in commercial orchards. Scion vigor is known to be affected by numerous factors including root hydraulic pressure, water uptake efficiency, hormone production, nutrient uptake, stomatal conductance, and intercellular CO₂ levels [40,56,72] and even within a single species, *Malus pumila*, there exists evidence supporting different mechanisms underlying dwarfing [39]. It is likely that in the case of dwarfing, as with many other rootstock-induced traits, multiple independent molecular pathways can result in similar scion phenotypes. Much is known about many other scion traits in general; however, the impact of rootstocks on these scion phenotypes remains unclear. For example, in apple tree scions the genetic underpinnings of tree architecture [73,74], hydraulic efficiency [75], and biennial bearing [76] have been documented. Work to date has demonstrated that rootstock genotype plays a role in shaping variation in these traits in the scion [77–79]; however, the relative roles of rootstock and scion as well as the mechanism underlying rootstock influence remain insufficiently understood. Expanding these studies to include questions such as the effect of rootstock diversity or molecular signaling during scion modulation presents exciting areas of future research.

In addition to altering tree architecture, rootstocks are widely used to confer resistance to pests and pathogens that affect the scion, including physiological disorders (reviewed in [40]). For instance, anthracnose resistance of avocado scions has been shown to be induced by rootstocks [80]. In this case, resistance is linked to increased diene concentrations, which may be due to improved scion nutrition. Improved nutrient and water uptake and transport by the rootstock to the scion is also thought to play a role in resistance to physiological disorders such as physiological pitting and stem-end browning in kiwi and stem-end rind breakdown in citrus [81,82].

Genetic Underpinnings of Rootstock Traits under Selection

Disentangling genetic and environmental components of desirable rootstock traits would allow marker-assisted selection to facilitate rootstock breeding [42]. Several studies have progressed toward this goal by generated segregating F1 mapping populations of rootstocks to which a common scion is grafted to identify the genetic basis of economically important traits of rootstocks that are expressed in the scion. Unlike annual crops, which are commonly inbred and genetically homozygous, in woody perennials genetic mapping often occurs in the F1 generation, for which the parents are typically highly heterozygous. In apple, studies exploring rootstock genetic contributions to dwarfing phenotypes led to the identification of the *Dwarfing 1* (*Dw1*) and *Dwarfing 2* (*Dw2*) loci [83,84]. Another study documented the genetic basis of absorption and translocation of nutrients by apple rootstocks and demonstrated significant rootstock effects on the transport of Ca, Cu, K, Mg, Mn, Na, P, S, Zn, and Mo [85]. In a similar experiment in grafted tomato, three to eight loci controlling salt tolerance from the rootstock genome were linked to increased yield in the scion [86–88]. Additional studies in grapevine identified loci in rootstocks that influence tolerance to lime-induced iron deficiency [89] and scion transpiration, leaf area, and water-use efficiency [90]. These pioneering studies and others provide convincing evidence of a genetic basis underlying rootstock modulation of scion phenotypes. Future work, including fine mapping, is needed to achieve a detailed understanding of the rootstock-genetic architectures of agriculturally important traits exhibited in the root and/or in the grafted scion. In addition, multisite, multiyear studies will facilitate deeper understanding of genotype \times environment interactions.

Scion Modulation of Rootstocks

While most agricultural grafting involves using rootstocks to influence phenotypes expressed in the scion, it is worth noting that grafting can also use scions to affect root system phenotypes, an approach that may be useful in some root/tuber crops. For example, grafting was developed in Indonesia in the late 20th century for cassava, using an inedible wild relative as the scion to improve yield [8]. In this 'Mukibat' system an arboreal *Manihot* species, *M. glaziovii*, is grafted onto the cultivated cassava *Manihot esculenta* [91]. This pairing increased the total yield of tubers by approximately 100% as well as tuber size [92]. Yield quality in sweet potato and potato have also benefited significantly through the application of grafted scions [93–95]. In tuber crops, effects on the rootstock are of particular significance for crop yield; in fruit crops scion effects on the rootstock have received less attention. However, scion effects on rootstocks are likely to be ubiquitous and large, as the flow of sugar, hormones, and nucleic acids into the root system has substantial effects on root growth, carbohydrate storage, and phenology [96,97] (as documented in Molecular Interactions below). In general, examining scion effects on rootstocks remains an important but woefully understudied component of rootstock–scion interactions.

Recent Advances and Future Directions in Rootstock Biology

Rootstocks can confer enhanced tolerance to abiotic and biotic stressors, providing a valuable mechanism to improve and expand perennial crop cultivation and global food production in the face of changing climatic conditions [42,37]. While these grafting-induced benefits are well understood from a physiological perspective, we have yet to build an integrated understanding of the molecular mechanisms that coordinate rootstock–scion communication and ultimately lead to enhanced crop traits. Many important aspects of rootstock biology are just beginning to take shape, including long-distance molecular signaling and the capacity of rootstocks to modulate interaction between plant and soil microbiomes.

Molecular Interactions

Grafting has enabled mass cultivation and improvement of woody perennial crops, but the generation of genetic chimeras through grafting also provides an important tool for understanding fundamental questions in plant biology. Multiple recent works have begun to shed light on

one such longstanding question: whether grafting induces heritable changes in the scion [98]. Revolutionary work from the Bock laboratory examining genomic interactions between sexually incompatible *Nicotiana* species showed that entire chloroplast and nuclear genomes can be bidirectionally transferred across the graft union, resulting in asexual hybrids between the rootstock and scion genotypes [29,30,99]. This phenomenon appears to be localized to tissues near the graft union and is therefore not heritable except in the rare event that an adventitious bud forms from one of these cells in the graft junction. Nevertheless, these studies demonstrate that, through as-yet-unknown mechanisms, large pieces of DNA or entire plastid genomes can traverse the graft junction, suggesting that it may be possible for these macromolecules to travel further into the scion under certain grafting conditions [100]. In addition to the movement of DNA itself, interspecific grafting within the Solanaceae has been shown to cause heritable changes in DNA methylation patterns in the scion [101]. This research also found changes in methylation of rootstock material, indicating that this is a reciprocal process across the graft junction. Collectively, this work suggests that future studies should focus on the graft transmissibility of heritable material and its impacts on plant form, physiology, and evolution.

Additionally, grafted plants offer unique arenas to investigate other pathways of long-distance communication between cells. While long-distance signaling may indirectly involve hormones, metabolites [102–104], or water and nutrient availability, other molecules – proteins, transcripts, and sRNAs – provide a direct link to underlying genetic mechanisms [105,106]. The extent to which these direct versus indirect long-distance signals coordinate grafting-induced improvements in the reciprocal half of the plant remains unclear. However, recent research lends substantial support for the direct involvement of mobile, mature sRNAs, which act as signals between the root and shoot targeting a wide range of transcripts and eliciting far-ranging graft-transmissible effects, from phosphate starvation response [107] to tuberization [97,108] to pest and pathogen resistance [109]. When mutant *Arabidopsis* rootstocks defective in sRNA biogenesis were grafted to wild-type scions, mature 22- and 24-nucleotide sRNAs accumulated in the roots, indicating that these sRNAs had been produced in the shoot and subsequently traversed the graft junction [110]. This experiment unequivocally demonstrated that mature sRNAs, and not simply sRNA precursors, are capable of long-distance transport, and has helped to answer longstanding questions regarding systemic, whole plant phenomena such as acquired virus resistance [111].

Beyond sRNAs, a growing body of work indicates that portions of the transcriptome itself are graft transmissible and the functional movement of individual transcripts (e.g., those inducing tuberization in a photoperiod-sensitive manner [96] or mediating morphological changes in traits such as leaf complexity [112,113]) has been demonstrated. Furthermore, recent work combining interspecific grafting with high-throughput RNA sequencing has revealed that a large fraction of the transcribed genome undergoes long-distance transport [114]. While the exact quantification of the mobile transcriptome varied from just over 2000 non-cell-autonomous transcripts between related *Arabidopsis* ecotypes [114] to almost half of the annotated gene space between *Arabidopsis* and the parasitic plant *Cuscuta* [115], these experiments clearly demonstrate that plant transcriptomes are spatially promiscuous.

The paradigm shift from a model of cell-autonomous to massively mobile transcript localization in plant molecular signaling raises new questions about mRNA transport and non-cell-autonomous mRNA function. Is there a ‘zip code’ that marks transcripts for long-distance movement and directs their end localization and, if so, how conserved across genetically distinct rootstocks and scions is the mechanism? Do mobile transcripts function to influence growth and development in their new location? Elegant work has identified RNA motifs that are required for the long-distance transport of *GIBBERELLIC ACID-INSENSITIVE* (*GAI*) transcripts [116]; whether these motifs can be universally extended to explain mass transcript trafficking remains to be seen.

Additional research has complemented transcriptomic profiling of graft-transmissible mRNAs with proteomics to demonstrate that many of the transported RNAs are indeed translated at their new location, suggesting that these mobile transcripts are capable of functioning after long-distance transport [114].

Growing support for long-distance, graft-transmissible molecular signaling in conjunction with rapid advances in genotyping and phenotyping technologies that allow us to hone in on the genetic mechanisms underlying enhanced abiotic and biotic stress tolerance has sparked interest in a new agronomic application of this ancient technique [117]. Transgrafting – the physical joining of a genetically engineered rootstock with a wild-type scion (or vice versa) – enables targeted crop protection without genetic alteration of the product [38]. This practice has been explored in both annuals such as watermelon (*Citrullus lanatus*) [118] and perennials such as apple (*Malus domestica*) [119], grape (*V. vinifera*) [120,121], citrus (*Citrus* spp.) [122], and cherry (*Prunus* spp.) [123] and shows promise for combating abiotic stressors such as salt and drought [122] as well as detrimental diseases affecting both scion and rootstock [118,120,121,123]. The efficacy of transgrafting is illustrated by a case study in grape, where the crippling decomposition of *V. vinifera* vasculature by *Xylella fastidiosa* (the causative agent of Pierce's disease) is apparently completely halted by the genetic fortification of rootstock cell walls [124]. Importantly, while modification of the *V. vinifera* rootstock was sufficient to confer protection on the scion, PCR assays demonstrate that this resistance was achieved without the movement of stable genetic material [38]. The widespread adoption of transgrafting may allow targeted crop protection without the direct modification of crop products.

While the vast majority of studies looking for graft-transmissible molecular signals have been performed in annual model systems, perennials provide a more agriculturally relevant basis for this line of research due to the extensive use of grafting in commercial vineyards and orchards. These long-lived 'fields' represent a valuable resource for exploring perennial-specific questions. For example, how does the composition and quantity of the mobile transcriptome change seasonally or from year to year? How does the environment, under real-world conditions, modulate the plasticity of long-distance communication in plants? Finally, beyond the movement of molecules, grafted perennials can also be used to study the graft transmission of both bacteria and endophytes.

Microbiomes of Rootstocks

Just as the study of rootstock genetics and domestication is in the early stages of understanding, so too are the effects of rootstocks on the plant microbiome. The emerging field of microbiome research provides evidence that rootstock–scion interactions are almost certainly influenced in part by the beneficial root microbiome, which includes fungal endophytes and plant growth-promoting (PGP) bacteria found within and around the root system. These microbes can influence uptake of micronutrients, generate hormones, create a root zone environment that is hostile to pests and pathogens, and impact plant phenotypes including disease [125], nitrogen, phosphorus and iron limitation, and resistance to heat, drought, and salt [126]. Additionally, members of the root microbiome can enter the plant and be transported via xylem to aerial tissues where they can act as biocontrol agents and impact stress response [127].

Research investigating the interactions of root microbiomes with shoot performance, specifically in grafted plants, is scarce. However, evidence from own-rooted grapevine has demonstrated that the bacterium *Burkholderia phytofirmans* strain PsJN can colonize the root system and, on transmission to the shoot, protects the vine from pathogenic *Botrytis* and *Pseudomonas* while also modulating carbohydrate metabolism and increasing freezing tolerance [128–131]. PGP bacteria have also been implicated in altering plant photosynthesis rate, transpiration, stomatal conductance, and internal leaf CO₂ [127].

Multiple biotic and abiotic factors impact the diversity and composition of the root microbiome. Some studies have suggested that abiotic factors play a large role in determining microbiome community structure, which is particularly relevant to cultivated species where the abiotic environment is often manipulated to enhance plant growth. For example, microbiome community structure associated with arid grassland ecosystems is driven not by the complexity of plant functional groups but rather by water availability [132]. Similarly, in studies examining *Cannabis* varieties, soil differences are implicated as a major contributor to microbiome community composition as a whole [133]. Compared with non-farmed desert land, farmed deserts show dramatic changes in microbiomes due to irrigation and concomitant loss of extremophile species [134–136]. These results indicate that abiotic factors, including those manipulated in agricultural settings, are often major drivers of microbiome communities in plants. However, evidence for plant genotype playing a role in microbiome community composition indicates that abiotic conditions are not the sole factor determining the microbiome. Experiments evaluating different grapevine-associated soil bacteria show that some (*Pseudomonas*, *Acinetobacter*, *Sphingobacterium*, *Enterobacter*, and *Delftia* sp.) have the ability to protect plants against simulated drought and produce biomass despite low water availability [127]. The magnitude of these benefits is dependent on stress treatment and the sensitivity of individual grapevine genotypes to drought. This research indicates that drought-sensitive rootstocks could be supplemented and modified by inoculating the soil with the beneficial bacterial strains identified in the microbiome of drought-tolerant rootstocks, increasing performance under drought conditions [127]. Similar evidence of genotype-specific fungal communities in the soil has been observed in crop fields of potato and wheat [137] and in greenhouse studies with *Cannabis* [133].

Ongoing studies demonstrate the ability of many plant species to actively select for the bacterial composition of the rhizosphere [138]. Roots modulate their microbiomes by exuding a complex mix of amino acids, organic acids, and sugars, a cocktail that functions both as a defense against pathogens and as a recruitment tool to foster the growth of beneficial microbes [139]. Concentrations and compositions of root exudates differ between plant species [140,141] and between varieties within species [142] and are also known to change in response to abiotic conditions. This variation provides selective niches that determine the species composition of plant microbiomes, perhaps similar to the ‘arms-race’ mechanism of plant pathogen–host evolution [143]. Although most of the research examining what root-based effects determine microbiome composition and structure have been conducted in annual crop systems, it is likely that perennial species similarly generate selective environments for beneficial microbes.

Current work reveals that the root microbiome can enhance plant productivity under stressful conditions, prevent infection from pathogenic bacteria, modify nitrogen availability and carbon storage, and have many other major biological impacts. However, it also raises new questions about rootstock microbiomes. Which combination of microbiome species and rootstock genotypes optimally alters the phenotype of the grafted plant? How permanent is the microbiome? Can inoculation be used to further leverage rootstock performance? How much of the root microbiome is transferred to the shoot microbiome? To what extent is recruitment of specific communities possible?

Concluding Remarks and Future Perspectives

This synthesis of our present knowledge of grafting and rootstock biology comes as there is growing interest in sustainably enhancing crop productivity to address challenges posed by global population growth and climate change [2,32,44]. For woody perennial species, which have long generation times and are often self-incompatible, traditional breeding practices employed in annual crops are usually infeasible. Rootstocks provide agriculturists with a mechanism by which to improve perennial crops and increase their productivity under harsh

Outstanding Questions

For a given woody perennial crop, what is the domestication history of its rootstocks? Which wild species contributed to the germplasm of cultivated rootstocks and what is their geographic distribution in nature?

What are the genetic underpinnings of phenotypic variation observed in the rootstock itself (e.g., root architecture, abiotic and biotic stress tolerance) and graft-transmissible effects on the scion? Are there scion-modulated traits in the rootstock and, if so, what is their genetic basis?

How are the genetic and phenotypic interactions between rootstock and scion affected by the environment?

What are the molecular signals (e.g., transcripts, sRNAs, proteins, metabolites, hormones) underlying graft-transmissible phenotypes? How far can large portions of DNA traverse the graft junction?

Is Darwin's concept of graft hybridization explained by epigenetics? Does grafting induce heritable epigenetic changes that alter important agronomic traits?

To what extent does the soil microbiome impact rootstock function and scion phenotype? Does the rootstock influence scion microbiome composition?

environmental conditions while simultaneously limiting agricultural inputs (irrigation, fertilizer, pesticides). In addition, this work provides a reference for comparison of grafting in annual crops, such as tomato and melons, for which the process is widely used to combat abiotic and biotic stresses as well as to boost scion vigor.

We advocate additional research in the molecular, evolutionary, and domestication processes of rootstock species using newly emerging technologies and analyses including high-throughput genomics and phenomics (see Outstanding Questions) [4,144]. The resulting data will address pertinent questions for rootstock biology, including rootstock diversity, the evolution of clonal, perennial crops under artificial selection, mechanisms underlying rootstock–scion interactions and graft compatibility, and the impact of root systems on economically important traits in the scion. Of particular interest is the development and maintenance of diverse living germplasm collections for woody perennials used as scions and rootstocks, as well as the construction of crosses and grafting experiments needed to facilitate additional work examining the genetic basis of traits in grafted crops. This complex task requires the identification of genes contributing to phenotypic variation in both the rootstock and the scion, genes that may be carried by the rootstock, the scion, or both. Genome-wide association mapping [145] and sequence-first population genomic approaches [146] offer promising avenues of exploration in perennials, which are often long-lived and highly heterozygous. Comprehensive germplasm collections, coupled with dynamic technological and analytical advances, have the potential to yield significant advances in grafted crops, which represent a key component of sustainable agriculture.

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