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Control of Fruit Tree Vigor Induced by Dwarfing Rootstocks

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ABSTRACT

Grafting of fruit trees has been practiced for more than two millennia, and dwarfing rootstocks have been used to control scion vigor for several centuries. The fact that most commercial temperate fruit trees are compound plants composed of two separate genotypes (the scion selected for fruit and shoot characteristics, and the rootstock selected for root characteristics) makes them interesting objects for studying root–shoot interactions in plants. The size-controlling effect of certain rootstocks in various fruit tree species is perhaps the most intriguing and commercially important example of how genetics of one part (the root) of compound plants can influence the behavior of the other part (the shoot). While there is no debate about the potential of rootstocks to affect the growth and productivity of the scion in compound fruit trees, there is no consensus on the physiological and/or anatomical mechanisms involved in the dwarfing phenomenon. Indeed, different hypotheses focusing on various aspects of plant function have been proposed to explain the dwarfing mechanism.

This review discusses the concepts and the experimental support for six of the primary theories proposed to explain the dwarfing mechanism induced by rootstocks in fruit trees. These theories are based on the idea that dwarfing is caused by semi-incompatibility between the rootstock and scion or anatomical, morphological, or physiological characteristics of the rootstock or graft union that affect tree water relations, tree nutrition, scion–rootstock hormonal and metabolic

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signaling, carbohydrate storage and mobilization, and/or the relative abilities of the scion and rootstock components of the tree to compete for resources.

Each of the proposed theories has received some experimentally based support in selected crops. Scion–rootstock semi-incompatibility is a general mechanism that may be involved in many scion–rootstock combinations and could cause responses that appear to involve the factors common to the other theories. None of the theories have been documented to be involved in all rootstock–scion combinations or to be solely responsible for the dwarfing response of scions associated with specific rootstocks. However, there is good evidence that changes in water relations are related to the dwarfing response in several species. In retrospect, it is perhaps unrealistic to think that any single one of these or other mechanisms could be solely responsible for orchestrating all of the complex interactions involved in rootstock-induced vigor reduction of the scion.

KEYWORDS: apple; carbohydrate; cherry; citrus; hormones/signals; incompatibility; kiwifruit; nutrition; peach; root–shoot interactions; source–sink competition; water relations

I. INTRODUCTION

Grafting as a propagation technique for fruit trees has been practiced for more than two millennia (Pease 1933; Mudge et al. 2009). The dwarfing potential of rootstocks has also been known for a long time. More than 2000 years ago, Alexander the Great (356–323 BCE) sent a dwarf apple tree from Persia (Iran) to the Lyceum (near Athens, Greece) (Fallahi et al. 2002). Theophrastus (370–285 BCE) also described a rootstock capable of dwarfing apple trees (Atkinson and Else 2005). The use in Europe of the dwarfing Paradise rootstock for apples was described by Johannes

Ruellius (1474–1537), a French physician and botanist, and later by John Parkinson (1567–1650), an English botanist (Jackson 2003). The French Paradise rootstock is thought to have originated in Armenia as a form of *Malus pumila* or as *M. pumila* × *M. sylvestris* (Jackson 2003). Already at that time, the very dwarfing Paradise (French Paradise) was reported as different from the less dwarfing Doucin rootstock (English Paradise) (Ferree and Carlson 1987). The distinction between Paradise and Doucin was kept throughout the nineteenth century, and in 1870, Thomas Rivers (1866), a famous English pomologist, reported 14 types of Paradise rootstocks. Rivers (1866) suggested that "the pear trees for dwarf fruit tree walls should be grafted on quince" (*Cydonia oblonga*) stocks. This suggests that the size-controlling potential of quince rootstocks for pear trees has been known for more than 150 years.

In 1912, researchers at the East Malling Research Station (England) started collecting rootstocks from around the world with the names of Paradise and Doucin in order to study, identify, and classify them. Hatton (1917) studied 71 collections from 35 sources and reclassified and described nine of them. He named these nine rootstocks with Roman numerals I–IX following the designation EM (that became later M). The rootstock that Hatton (1917) classified as EM.IX was selected as a seedling in 1879 in France and called Paradis Jaune de Metz (Ferree and Carlson 1987; Masseron 1989). This rootstock, later called M.9, became the protagonist first for the profound modification of apple culture worldwide, and later for fruit tree cultivation in general (Webster 2001). Indeed, the introduction of dwarfing rootstocks allowed for shorter fruit trees that were more easily managed from the ground without the use of ladders and led to decreased labor costs needed for orchard management (Webster 2002). It is well known that much of the annual production costs for fruit trees depend on the costs of hand labor for pruning, fruit thinning, and harvest. For instance, in four peach production systems, ladder work for fruit harvest, fruit thinning, and tree pruning accounted for more than 80% of the system-specific production costs at orchard maturity (DeJong et al. 1999). Klonsky (1994) reported that in kiwifruit, labor costs account for almost 70% of the preharvest costs and for around 50% of total production costs per hectare.

Size-controlling rootstocks may decrease labor costs needed for pruning not only because trees are shorter and thus manageable from the ground level without the use of ladders, but also because they can decrease the amount of cuts needed to prune each tree. Size-controlling rootstocks significantly decrease the amount of wood removed with prunings compared to trees on invigorating rootstocks (Loreti et al. 2001; DeJong et al. 2004). Reduced requirements for pruning trees on dwarfing rootstocks have been related to decreased amounts of excessive watersprouts (epicormic shoots) in peach trees (Basile et al. 2003a). In peach trees, watersprouts are usually removed by summer and/or dormant pruning, and the number of watersprouts per tree directly affects the number of cuts pruners have to make on each tree, which affects the time needed for pruning.

Even though size-controlling rootstocks for apples and pears have been used for a long time, understanding of the physiological mechanisms of rootstock-mediated vigor control is still unclear. This lack of understanding has been one of the reasons why it has taken so long for breeders to provide commercial size-controlling rootstocks for some important fruit tree species like peach, sweet cherry, plum, and apricot. Breeding programs for dwarfing apple rootstocks have been carried out in many places around the world to find more dwarfing rootstocks than the widely planted M.9 (Vercammen 2004a; Vercammen and Gomand 2011). There is a need to find alternatives to M.9 and other M series rootstocks because of their high susceptibility to fireblight and other diseases and because tree growth on some of the more dwarfing rootstocks quickly declines with cropping, resulting in the need for replanting (Vercammen and Gomand 2011). Similarly, in pears, different programs around the world have aimed to find new dwarfing rootstocks to use as an alternative to clonal quince rootstocks that are sensitive to lime-induced chlorosis and fireblight, have limited cold hardiness, or are incompatible with many scion cultivars (Brewer and Palmer 2011). During the last 40 years, different breeding programs from around the world have provided numerous size-controlling rootstocks for sweet cherry (Webster 1980, 1993, 2001; Vercammen 2004b), apricots (Knowles et al. 1994), plums (Webster 1980, 1993, 2001), and peaches (Fideghelli 2002; Reighard 2002; DeJong et al. 2005). Most of these rootstocks were developed from either intra- or interspecific hybridizations (Tables 2.1 and 2.2). Tables 2.1 and 2.2 contain references to some of the more important rootstocks, and additional information can be found in Rom and Carlson (1987), Webster and Wertheim (2003), Jackson (2003), Reighard and Loreti (2008), and Marini and Fazio (2017).

II. BIOLOGICAL COMPLEXITY OF GRAFTED FRUIT TREES AND ROOTSTOCK–SCION INTERACTIONS

Most cultivated fruit trees in Europe and the USA are composed of commercial cultivars (scion) grafted on commercially available rootstocks. Therefore, most cultivated fruit trees involve two genetically

Table 2.1 Series name, origin/parentage, and source of dwarfing rootstock for apple and pear.

Series name	Rootstock name	Origin/parentage	Source	Reference
Apple				
Malling	M.7	Doucin (English Paradise apple)	East Malling (UK)	Hatton 1917
	M.9	French Paradise apple 'Jaune de Metz'	East Malling (UK)	Webster and Wertheim 2003
	M.26	M.16 × M.9	East Malling (UK)	
	M.27	M.13 × M.9	East Malling (UK)	
M.9 subclones	M.9 EMLA	Virus-free M.9 subclone	East Malling and Long Ashton stations (UK)	Webster and Wertheim 2003
	M.9 Fleuren 56	Selection of M.9	The Netherlands	
	M.9 NAKB 337	Selection of M.9	The Netherlands	
	M.9 Pajam1	Selection of M.9	France	
Malling-Merton	MM.106	'Northern Spy' × M.1	East Malling and John Innes Centre, Merton (UK)	Preston 1955
P	P.22	M.9 × 'Antonovka'	Research Institute of Pomology and Floriculture, Skierniewice (Poland)	Zurawicz et al. 2011
	P.63	M.9 × 'Alnarp 2'		
Budagovsky	B.9	M.8 × 'Red Standard'	Michurin College of Horticulture (Russia)	Webster and Wertheim 2003
	B.491	Unknown	Michurin College of Horticulture (Russia)	
Supporter	Supporter 1	M.9 × *Malus baccata*	Institut für Obstforschung Dresden-Pillnitz (Germany)	Fischer 1997
	Supporter 2	M.9 × *Malus micromalus*	Institut für Obstforschung Dresden-Pillnitz (Germany)	
	Supporter 3	M.9 × *M. micromalus*	Institut für Obstforschung Dresden-Pillnitz (Germany)	
Cornell-Geneva	G.16	Ottawa 3 × *Malus floribunda*	Cornell University, Geneva (USA)	Clark and Finn 2006
	G.41	M.27 × 'Robusta 5'	Cornell University, Geneva (USA)	
MAC	MAC 9	Open pollinated seedling from M.9	Michigan State University (USA)	Ferree and Carlson 1987

(*continued*)

Table 2.1 (Continued)

Series name	Rootstock name	Origin/parentage	Source	Reference
Pear				
Clonal quince	EMA	Angers type *Cydonia oblonga*	East Malling (UK)	Jackson 2003
	EMC	Angers type *C. oblonga*	East Malling (UK)	
	EMH	Angers type *C. oblonga*	East Malling (UK)	
	Sydo	Angers type *C. oblonga*	INRA (France)	
	BA 29	Provence type *C. oblonga*	INRA (France)	
	Adams 332	Angers type *C. oblonga*	Belgium	
Old Home × Farmingdale	OH × F 40	'Old Home' × 'Farmingdale'	Oregon State University, Corvallis (USA)	Hummer 1998
	OH × F 69	'Old Home' × 'Farmingdale'	Oregon State University, Corvallis (USA)	
Fox	Fox 11	Open pollinated seedlings from *Pyrus communis*	University of Bologna (Italy)	Quartieri et al. 2011
	Fox 16		University of Bologna (Italy)	
Rhenus	Pyrodwarf	'Old Home' × 'Bonne Luise d'Avranches'	Geisenheim Research Institute (Germany)	Jacob 1998

The list is not intended to include all the developed dwarfing rootstocks.

Table 2.2 Series name, origin/parentage, and source of dwarfing rootstock for peach and cherry.

Series name	Rootstock name	Origin/parentage	Source	Reference
Peach				
P.S.	P.S.A5	Seedling of *Prunus persica*	University of Pisa (Italy)	Loreti and Massai 2006a
	P.S·B2	Seedling of *P. persica*	University of Pisa (Italy)	
Mr.S.	Mr.S. 2/5	*Prunus cerasifera* × *P. spinosa*(?)	University of Pisa (Italy)	Loreti et al. 1990
I.S.	I.S. 5/22	Open pollinated seedling from GF557	University of Pisa (Italy)	Loreti and Massai 1998
	I.S. 5/19	Open pollinated seedling from GF557	University of Pisa (Italy)	Loreti and Massai 2006b
	I.S. 5/8	Open pollinated seedling from GF557	University of Pisa (Italy)	
Spanish	Adarcias	*Prunus dulcis* × *P. persica*	EEAD (Zaragoza, Spain)	Moreno and Cambra 1994
	Adesoto 101	Open pollinated seedling from *Prunus insititia*	EEAD (Zaragoza, Spain)	Moreno et al. 1995
	Montizo	Open pollinated seedling from *P. insititia*	SIA-DGA (Zaragoza, Spain)	Felipe et al. 1997
	Monpol	Open pollinated seedling from *P. insititia*	SIA-DGA (Zaragoza, Spain)	
INRA	GF655/2	Open pollinated seedling from *P. insititia*	INRA (France)	Layne 1987
	Damas 1869	*Prunus domestica* × *P. spinosa*	INRA (France)	Reighard and Loreti 2008
	Ishtara	(*P. cerasifera* × *P. salicina*) × (*P. cerasifera* × *P. persica*)	INRA (France)	
	Julior	*P. insititia* × *P. domestica*	INRA (France)	
Controller™5	K146-43	*Prunus salicina* × *P. persica*	University of California, Davis (USA)	DeJong et al. 2011
Controller™9	P30-135	*P. salicina* × *P. persica*	University of California, Davis (USA)	
Controller™6	HBOK 27	*P. persica 'Harrow Blood'* × *'Okinawa'*	University of California, Davis (USA)	Tombesi et al. 2011
Controller™7	HBOK 32	*P. persica 'Harrow Blood'* × *'Okinawa'*	University of California, Davis (USA)	
Krymsk	VVA-1	*Prunus tomentosa* × *P. cerasifera*	Krymsk Breeding Station (Russia)	Reighard and Loreti 2008
	VSV-2	*P. incana* × *P. tomentosa*	Krymsk Breeding Station (Russia)	

(*continued*)

Table 2.2 (Continued)

Series name	Rootstock name	Origin/parentage	Source	Reference
Cherry				
GiSelA	GiSelA 5	*P. cerasus* × *P. canescens*	Justus University of Giessen (Germany)	Franken-Bembenek et al. 1999
	GiSelA 6	*P. cerasus* × *P. canescens*	Justus University of Giessen (Germany)	
Weiroot	W.72	Open pollinated seedling from *Prunus cerasus*	Weihenstephan University (Germany)	Schimmelpfeng and Liebster 1979
	W.53	Open pollinated seedling from *Prunus cerasus*	Weihenstephan University (Germany)	
GM	GM.9	*Prunus incisa* × *P. serrula*	Gembloux Research Station for Fruit and	Trefois 1985
	GM.61/1	*Prunus dawyckensis*	Vegetables (Belgium)	
	GM.79	*Prunus canescens*	Vegetables (Belgium)	

The list is not intended to include all the developed dwarfing rootstocks.

different genotypes (scion and rootstock) and are complex biological systems. Rootstock–scion relationships have been the subject of much research (Roberts 1949; Rogers and Beakbane 1957; Tukey 1964; Tubbs 1973a,b; Jones 1984; Webster 2004). The rootstock can affect nutrient concentrations in leaves (Brown and Cummins 1989; Boyhan et al. 1995), dormant stems (Knowles et al. 1984), flowers (Zarrouk et al. 2005), and fruit (Caruso et al. 1996); precocity of cropping (Webster and Hollands 1999; Whiting et al. 2005); bloom date (Durner and Goffreda 1992); rate of flower opening (Webster 1995); percent of leaf budburst (Maneethon et al. 2007); fruit set (Webster and Hollands 1999); fruit yield (Bussi et al. 1995); yield efficiency (Hudina et al. 2006); fruit quality (Castle 1995; Caruso et al. 1996; Sharma and Saxena 2004; Al-Jaleel et al. 2005; Giorgi et al. 2005; Scalzo et al. 2005; Whiting et al. 2005; Remorini et al. 2008); leaf net photosynthesis (Ferree and Barden 1971; Fallahi et al. 2002); tree susceptibility to frost damage (Tsipouridis and Thomidis 2005); tree resistance to plant diseases (Norelli et al. 2003; Bordignon et al. 2004); branch crotch angle (Layne et al. 1976; Crabbé 1984; Warner 1991); bark thickness (Yadava and Doud 1978); trunk cross-sectional area (Loreti et al. 1989); tree height and shoot length (Tworkoski and Miller 2007); leaf size and weight (Ferree and Barden 1971); and canopy volume (Hudina et al. 2006).

A. Effects of Size-Controlling Rootstocks on Vegetative Growth

Among the different rootstock effects, control of scion growth and vigor is one of the most fascinating phenomena. Size-controlling rootstocks can affect different features of vegetative growth of fruit trees. Generally, vigor-controlling rootstocks cause a decrease in tree crown dimension (Webster 1980; Webster and Hollands 1999; Lliso et al. 2004; Hudina et al. 2006) and tree height (Tworkoski and Miller 2007). Rootstock control of canopy vigor is often associated with a decreased scion trunk cross-sectional area (TCSA). Indeed, comparison of TCSA increase is often used as an allometric indicator of vigor of whole fruit trees (Pearce 1952; Khatamian and Hilton 1977), even though this parameter alone may not be sufficient to completely describe tree vigor (Nesme et al. 2005). For instance, Knowles et al. (1994) reported that, eight years from planting, TCSAs of ‘Sundrop’ apricot trees grafted on P.S.A. 5, P 1609, GF 655/2, Marianna 9.52, and Pixy were, respectively, 38, 41, 49, 50, and 78% of trees on the invigorating Marianna 6.64. At the end of six growing seasons, ‘Flavorcrest’ peach trees trained to a KAC-V (DeJong et al. 1994) and grafted on K146-43, Hiawatha, and P130–35 had TCSAs that were 59, 80, and 93%, respectively, of trees grafted on standard Nemaguard rootstock (DeJong et al. 2004). Similarly, 11 years after planting, TCSAs of 'Cox's Orange Pippin' apple trees grafted on P.2, M.27-EMLA, M.9-EMLA, and M.106-EMLA were, respectively, 30, 36, 58, and 85% of trees on P.18 (Webster and Hollands 1999). Similar effects have been reported for dwarfing rootstocks of sweet cherries (Whiting et al. 2005), plums (Boyhan et al. 1995), mandarins (Tsakelidou et al. 2002), oranges (Wutscher and Bistline 1988), and pears (Wertheim 2002). The effect of dwarfing rootstocks on TCSA is clearly cumulative with time, and differences in this parameter between trees grafted on rootstocks with contrasting vigor tend to increase with time from orchard establishment. Whiting et al. (2005) reported that, after two growing seasons in open field, TCSA was not significantly different among 'Bing' cherry trees grafted on Mazzard, GiSelA 5, and GiSelA 6, but differences became significant the following year and progressively increased until the end of the experiment (eight years after tree planting), when trees on GiSelA 5 and GiSelA 6 had a "cumulative" decrease in TCSA to 54 and 80%, respectively, of trees grafted on Mazzard rootstock. Similarly, differences in TCSAs between peach trees grafted on six seedling rootstocks increased with time after planting (Layne et al. 1976). However, one-year-old peach trees grafted on the size-controlling K146-44 already had a TCSA that was 25% of that of trees on Nemaguard (measurements were taken five months after transplanting one-year-old grafted trees in open field) (Basile et al. 2003b).

Stem extension growth can also be strongly affected by size-controlling rootstocks. Indeed, the effects of rootstocks with differing vigor on TCSA and on shoot length are strongly correlated (Hirst and Ferree 1995). Nine-year-old 'Cox's Orange Pippin' apple trees grafted on the very dwarfing M.27 had final mean shoot lengths that were only one-fourth of those of trees grafted on the invigorating MAC 9 (Webster 1995). Weibel et al. (2003) measured the effect of peach rootstocks with differing vigor control potential on the growth of different kinds of 'Loadel' and 'Flavorcrest' peach shoots (basal shoots arising from fruiting shoots, terminal shoots arising from fruiting shoots, and shoots arising directly from scaffolds) and showed that size-controlling rootstocks had differential effects on different types of shoots. The effect of dwarfing rootstocks on shoot growth has been associated with a reduced shoot extension growth rate in 'Crimson Lady' peach and 'Mayfire' nectarine trees grafted on size-controlling rootstocks compared to trees on vigorous rootstocks (Basile et al. 2003a; Solari et al. 2006a).

The dwarfing phenomena in a wide range of fruit trees are often associated with short internodes (Brown et al. 1994; Weibel et al. 2003).

Fruit trees in which the scion cultivar is genetically dwarfed have shorter internodes than standard trees (Faust 1989; Fideghelli et al. 2003). Similarly, dwarf trees induced by treatments with exogenous plant growth regulators are characterized by shorter internodes compared to untreated trees (Webster 2002). However, the relative importance of decreasing internode length in the whole dwarfing phenomenon induced by the rootstock is still questionable (Webster 2004). In an architectural study on 'Royal Gala' trees with differing dwarfing and invigorating interstock–rootstock combinations, Seleznyova et al. (2003) reported that, in general, node number and internode length significantly decreased from the most invigorating ('Royal Gala' on MM.106) to the most dwarfing interstock–rootstock combination ('Royal Gala' on M.9/M.9). However, the same authors reported that, independent of the interstock–rootstock combination, shoot length and mean internode length were strongly related to the number of nodes, and, because of the significance of these relationships, the differences in internode length between vigorous and nonvigorous interstock–rootstock combinations were not significant when shoots with the same number of nodes were compared. Similarly, Poll (1973) reported that internode length varies within the same cultivar and is strongly related to shoot length. This suggests that any analysis of the effects of any treatment on internode length always needs to take shoot length into account. In cherries, Prassinos et al. (2009) reported that differences in shoot growth between trees on rootstocks with different vigor were mainly due to changes in the number of internodes and not to differences in internode length.

Furthermore, the length of the growing period can be affected by rootstocks with differing vigor-controlling potentials, and this influence (together with the rootstock effect on shoot extension rate) can play an important role in determining final shoot length. Weibel et al. (2003) reported that the basal stems arising from hangers of bearing peach trees grafted on the size-controlling K146-43 and K146-44 rootstocks stopped growing significantly earlier than in trees on Nemaguard. Similarly, the growth of early shoots of bearing 'Worcester Pearmain' apple trees grafted on M.9 terminated significantly earlier than trees on M.2 (Avery 1969). Similar results have been reported for cherry trees grafted on GiSelA 5 (Prassinos et al. 2009).

In addition to shoot growth, another important component of total-tree vegetative growth is the number of growing points available in the canopy. It is clear that if rootstocks with differing size-controlling potentials affect the number of nodes per shoot and/or internode length, a rootstock effect on the total axillary vegetative buds per tree (potential growing points) for successive-year growth is also reduced. Weibel et al. (2003) reported that the number of one-year-old shoots per tree and the number of current-season lateral shoots per tree significantly decreased from trees grafted on the invigorating Nemaguard (1276 and 888 shoots per tree, respectively) to trees on the size-controlling K146-44 (628 and 142 shoots per tree, respectively). Similarly, Seleznyova et al. (2003) reported that the number of annual shoots per branch was significantly less in apple trees on M.9 than in trees on MM.106. These effects often compound, with the influence of size-controlling rootstocks on shoot growth causing a decrease in total-tree shoot growth (Avery 1969; Weibel et al. 2003).

Two other important components of total-tree shoot growth are the percentage of bud-break and the amount of sylleptic growth (secondary and tertiary lateral shoot growth). Percentage of budburst is strongly affected by the fulfilling of chilling requirements and by apical dominance. Peach rootstocks with chilling requirements higher than that of the scion cultivar can decrease budburst when chilling requirements are not entirely fulfilled (Maneethon et al. 2007). However, this effect does not appear to be directly associated with size-controlling potential of the rootstock (Maneethon et al. 2007). Seleznyova et al. (2003) did not find any significant effect of rootstocks with different dwarfing capacity on the percentage of budburst.

Apical dominance (correlative inhibition) also suppresses the growth of axillary buds located on actively growing stems (sylleptic growth). The strength of correlative inhibition is species and cultivar specific. For instance, correlative inhibition is stronger in cherries and apples than in peaches and apricots. In addition, the degree of correlative inhibition also strongly differs among cultivars of apples and pears (Jackson 2003). Rootstocks can affect the amount of sylleptic growth and thus may alter the degree of correlative inhibition. Dwarfing rootstocks have been reported to decrease sylleptic growth in apples (van Hooijdonk et al. 2010), cherries (Cook et al. 2004), and peaches (Pernice et al. 2006) compared to invigorating rootstocks.

Size-controlling rootstocks also can strongly affect crown architecture by changing the proportion of different types of shoots within a canopy. Apple trees grafted on M.9 had more bourse shoots (sylleptic shoots subtending flower clusters) with fewer nodes than trees grafted on MM.106 (Seleznyova et al. 2003). Peach trees grafted on size-controlling rootstocks generally have fewer watersprouts per tree than trees on the invigorating Nemaguard (Basile et al. 2003a; Pernice et al. 2006). Similarly, Clearwater et al. (2006) reported that 'Hort16A' kiwifruit vines grafted on size-controlling rootstocks (*Actinidia kolomikta* and *A. polygama*) had a higher proportion of terminating shoots compared to vines on invigorating rootstocks (*A. hemsleyana*). In addition, they found that terminated parent shoots in the following year produced a higher proportion of daughter terminated shoots than long parent shoots. Therefore, the effect of these kiwifruit rootstocks on vine vigor was cumulative over years. The results from Seleznyova et al. (2003) also indicate that apple rootstock effects on scion growth are strongly cumulative over time.

Genetic dwarfism in scions of fruit trees is often associated with wide branching angles (Faust 1989; Fideghelli et al. 2003). This appears to be common for apple (Warner 1991; Webster 2004; Tworkoski and Miller 2007) and has also been reported for sweet cherry (Osterc and Spethmann 2002). However, Weibel et al. (2003) did not detect any significant effect of size-controlling peach rootstocks on the branching angles with two peach scion cultivars ('Flavorcrest' and 'Loadel').

Most of the effects of dwarfing rootstocks on vegetative activity described in this chapter are subject to strong interactions with other factors. For instance, Tworkoski and Miller (2007) compared the vegetative growth of six apple scions with different growth habits (upright-round, upright-narrow, spreading-round, spreading-weep, 'Golden Delicious', and 'Delicious') grafted on four rootstocks with different dwarfing capacities (M.9, M.7, MM.111, and seedling) and reported that the vigor-controlling potential of the rootstock significantly interacted with the growth habit of the scion cultivar. Factors affected were shoot extension growth, tree height, canopy diameter, trunk diameter, number of nodes of one-year-old shoots, basal diameter of one-year-old shoots, internode length of one-year-old shoots, and number and length of branches. Similarly, peach rootstock effects on shoot growth were significantly affected by the scion cultivar (Weibel et al. 2003). Also, the training system can modify the effect of the rootstock on vegetative growth (DeJong et al. 2004). For instance, open vase 'Loadel' peach trees on the dwarfing K146-44 rootstock induced a 40% decrease in trunk circumference compared to trees on Nemaguard, whereas, when trees were trained to a perpendicular V, K146-44 induced a 30% decrease in trunk circumference. In the same study, 'Flavorcrest' trees on the K146-44 rootstock induced a decrease in tree vigor of around 40% independent of the training system. Costes and García-Villanueva (2007) reported that the strength of some influences of the dwarfing M.9 rootstock on crown architecture also differed depending on the apple scion cultivar. The effect of the rootstock on vegetative growth has also been reported to be affected by planting density (Loreti et al. 1993) and by water stress (Psarras and Merwin 2000).

III. PHYSIOLOGY OF THE DWARFISM INDUCED BY ROOTSTOCKS IN FRUIT TREES

As stated in this chapter, the physiological mechanism underlying the effect of vigor-controlling rootstocks on tree growth is not well understood, even though dwarfing rootstocks have been used for a long time and numerous experiments have been carried out to elucidate the dwarfing mechanism.

Several hypotheses have been proposed and tested to explain the dwarfing effect by means of different physiological mechanisms. All of them are based on the assumption that shoots and roots strongly influence each other, because of their complementary and dependent functions (functional equilibrium theory; Richards and Rowe 1977). In fact, shoots depend on roots for the supply of water and nutrients, whereas shoots provide the root system with carbohydrates, and both shoots and roots produce specific hormonal compounds that are believed to have a role in controlling and/or coordinating their activities (Jackson 2003). Previous reviews on dwarfing rootstocks have primarily focused on apple and pear rootstocks and have not included some of the mechanistic theories about the cause of dwarfing that are more prevalent currently (Atkinson and Else 2001; Jackson 2003; Webster 2004). This review will analyze the six theories concerning dwarfing rootstocks that are most prevalent for different fruit tree species: the semi-incompatibility theory, the water relations theory, the nutritional theory, the hormonal/signaling theory, the carbohydrate reserve theory, and the competition/architecture theory. In addition, other possible hypotheses and their putative contributions to the dwarfing mechanism will be briefly described.

A. The Semi-incompatibility Theory

The semi-incompatibility theory involves the idea that decreased growth or vigor of the scion of trees grown on specific rootstocks is caused by partial incompatibility between the scion and the rootstock. Scion–rootstock incompatibility in fruit trees is a common phenomenon that can occur between specific scion–rootstock combinations (Hartmann et al. 2002; Pina and Errea 2005). Most incompatibility phenomena are apparent within a few days after grafting, but sometimes incompatibility symptoms are minor, do not result in total dysfunction, and may become manifest several months or even several years after grafting (Eames and Cox 1945; Errea et al. 1994; Hartmann et al. 2002). The latter is often referred to as "delayed incompatibility" (Hartmann et al. 2002). Independent of the time when incompatibility becomes manifest, altered development of the structures at the graft union (especially of the conducting systems) often occurs in trees made of partially incompatible scion–rootstock combinations (Simons 1987; Errea et al. 1994; Salvatierra et al. 1998; Hartmann et al. 2002). Several authors have proposed that such morphological anomalies at the graft union may hinder the transport of water, nutrients, carbohydrates, and hormones across the union (Moing et al. 1990; Moing and Gaudillère 1992; Hartmann et al. 2002; Nakano et al. 2004). Sometimes, these effects may appear to be insignificant. For instance, Schmitt et al. (1989) reported that midday leaf water potential of cherry trees varied on trees with different scion–rootstock combinations (*Prunus avium* cv. 'Sam' on three clones of *P. cerasus* rootstocks and a *P. acida* rootstock, with *P. avium* F 12/1 rootstock as the control), and the variation in leaf water potentials was related to differing compatibility as indicated by visual leaf wilting.

The semi-incompatibility theory asserts that rootstock-induced dwarfing in fruit trees can be caused by partial incompatibilities that occur in specific size-controlling scion–rootstock combinations because the transport of water, solutes, and/or hormones across the graft union is altered. This hypothesis is supported by several studies (Simons and Chu 1984; Simons 1986, 1987; Ussahatanonta and Simons 1988; Soumelidou et al. 1994a) that have reported morphological and/or developmental anomalies (e.g. small vessels, swirling of vascular tissue, presence of necrotic areas, and large amounts of nonconducting phloem) in the vascular system at the graft union of trees on dwarfing apple rootstocks. Phenols can also play an important role in graft incompatibility in fruit trees (Errea 1998), and they are thought to be implicated also in dwarfism induced by the rootstocks (Faust 1989), but their mechanistic role is not clear (Lockard and Schneider 1981). The semi-incompatibility theory is often visually supported by strong over- or undergrowth of the scion relative to the rootstock in the field, by excessive rootstock suckering below the graft union, or by premature leaf coloring or abscission (Hartmann et al. 2002). There is little dispute that some scion dwarfing can be caused by partial scion–rootstock incompatibilities with specific scion–rootstock combinations when the signs of incompatibility are readily apparent. But it is often not clear whether the decreased growth of the scion is related to one of the other physiological theories described in this chapter.

B. The Water Relations Theory

The water relations theory asserts that the scions of trees grafted on vigor-controlling rootstocks are subjected to slight water stress conditions (compared to scions on vigor-inducing rootstocks) because of restricted water flow through the graft union or an inefficient water supply from the root system (Figure 2.1). It is well documented that water availability affects plant growth (Hsiao 1973) and even that regulated deficit irrigation scheduling that induces moderate water stress may be used to control vegetative growth of fruit trees (Chalmers et al. 1981; Marsal et al. 2002). Furthermore, it is clear that daily patterns in shoot growth of fruit trees are directly linked to temperature and changes in stem water potential (Berman and DeJong 1997). The water relations theory was proposed by Beakbane (1956) and is supported by numerous researchers working on several different tree crop species (Table 2.3). Early anatomical studies showed that dwarfing apple rootstocks tended to have roots with fewer and smaller xylem vessels

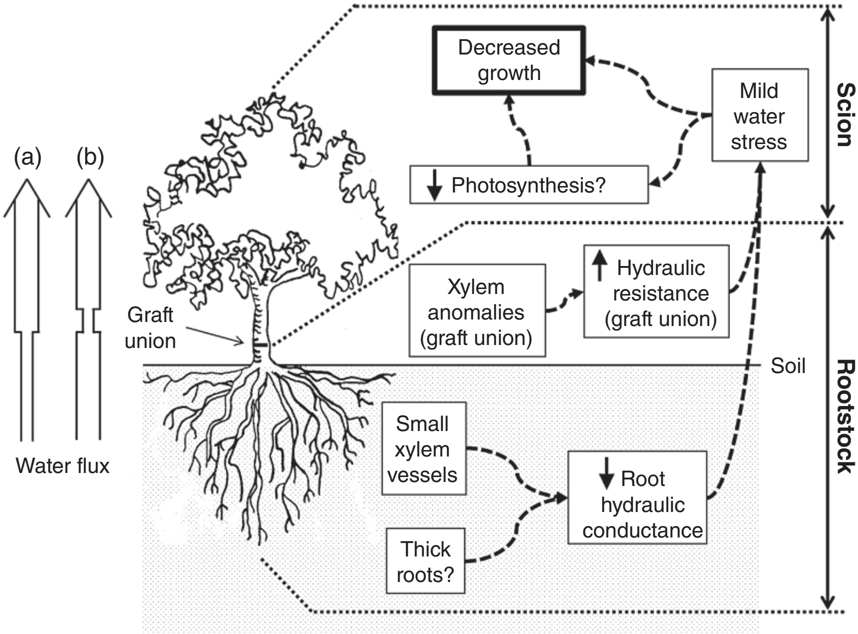

Figure 2.1 Schematic of potential water relations–mediated size-controlling mechanisms for trees grafted on dwarfing rootstocks. The arrows on the left side of the figure indicate that the restriction to water movement may be a function of the entire root system (a) or limited to the graft union (b).

than invigorating rootstocks (Beakbane and Thompson 1939). However, Rogers and Beakbane (1957) dismissed the idea that xylem anatomical differences could be involved because the prevailing view at the time was that xylem vessels were in substantial excess compared to what was necessary to efficiently move water through a tree.

One of the first experimental confirmations of the water relations theory was when Giulivo and Bergamini (1982) reported that midday leaf water potentials of ‘Golden Delicious’ apple trees grafted on dwarfing M.9 and M.26 rootstocks were significantly lower than those of trees on vigorous M.11 and seedling rootstocks, whereas trees with intermediate-high vigor (grafted on MM.111, MM.104, MM.106, and M.7) had intermediate values. Later, in more complete studies, Olien and Lakso (1984, 1986) provided convincing evidence that midday stem water potential measured on apple trees grafted on dwarfing M.9 and M.26 dwarfing rootstocks was significantly lower than that of trees grafted on more vigorous rootstocks (MM.104, M.7, and MM.106). These results were subsequently confirmed by Cohen and Naor (2002).

Peach trees grafted on K146-43 dwarfing rootstock also had lower midday stem water potentials than trees on the invigorating Nemaguard rootstock (Basile et al. 2003a). This result was confirmed by Solari et al. (2006a) with ‘Maycrest’ peach trees grafted on the same rootstocks used by Basile et al. (2003a). Similarly, Motisi et al. (2004) reported that midday xylem water potential measured at different heights above the graft union of ‘Armking’ peach trees grafted on dwarfing MrS 2/5 was significantly lower than for trees on the more invigorating GF677. Gonçalves et al. (2006) reported that stem water potential of sweet cherry trees grafted on vigorous rootstocks also was significantly higher than that of trees on dwarfing rootstocks. In contrast, Clearwater et al. (2004) did not find any correlation between kiwifruit rootstock vigor-controlling behavior and xylem water potential measured at different places in the canopy. Indeed, vines grafted on the *A. kolomikta* rootstock (a low-vigor rootstock) had lower xylem water potential than vines on *A. macrosperma* and *A. hemsleyana* (two vigorous rootstocks), but xylem water potential of vines on *A. polygama* (another low-vigor rootstock) was higher than that of vines on the two vigorous rootstocks. Similarly, Nardini et al. (2006) did not find any significant difference in midday leaf water potential between ‘Leccino-Minerva’ olive trees grafted on the dwarfing ‘Leccino Dwarf’ rootstock and trees grafted on the standard ‘Leccino-Minerva’.

Basile et al. (2003a) demonstrated that the rootstock effect on the peach shoot extension growth rate was significantly related to the

Table 2.3 Experimental evidence supporting the six theories formulated to explain rootstock-induced vigor reduction in apple, cherry, citrus, kiwifruit, olive, and peach.

	Theory					
Species	Incompatibility	Water relations	Nutritional	Hormonal/signaling	Carbohydrate reserves	Competition/ architecture
Apple	Simons and Chu 1984 Simons 1986, 1987 Ussahatanonta and Simons 1988 Soumelidou et al. 1994a	Beakbane and Thompson 1939 Beakbane 1956 Giulivo and Bergamini 1982 Olien and Lakso 1984, 1986 Cohen and Naor 2002 Atkinson et al. 2003 Iwanami et al. 2009 Bauerle et al. 2011	Ruck and Bolas 1956 Bukovac et al. 1958 Jones 1971, 1976, 1984 Fallahi et al. 2001 Neilsen and Hampson 2014	Gur and Samish 1968 Ibrahim and Dana 1971 Kender and Carpenter 1972 Yadava and Lockard 1977 Lockard and Schneider 1981 Soumelidou et al. 1994b Kamboj et al. 1997a,b, 1999a,b Jensen et al. 2003, 2010 van Hooijdonk et al. 2010, 2011 Zhang et al. 2015 Harrison et al. 2016		Avery 1969 Jackson 2003 Lauri et al. 2006 Costes and García-Villanueva 2007 Seleznyova et al. 2008 Foster et al. 2014

Cherry	Olmstead et al. 2006a,b Gonçalves et al. 2007 Meland et al. 2007	Gonçalves et al. 2006	Neilsen and Kappel 1996 Moreno et al. 2001	Prassinos et al. 2009	Olmstead et al. 2010	
Citrus		Syvertsen 1981 Syvertsen and Graham 1985 Vasconcellos and Castle 1994 Rodríguez-Gamir et al. 2010		Saidha et al. 1983 Noda et al. 2000		Lliso et al. 2004
Kiwifruit		Clearwater et al. 2007	Thorp et al. 2007			
Olive		Nardini et al. 2006				
Peach		Basile et al. 2003a,b Motisi et al. 2004 Solari and DeJong, 2006 Solari et al. 2006a,b,c Tombesi et al. 2010a,b, 2011 Bruckner and DeJong 2014		Sorce et al. 2002	Weibel et al. 2011	

rootstock effect on the daily oscillation of stem water potential measured early in the growing season and that vegetative growth was significantly correlated with cumulative stem water potential differences associated with different rootstocks over the growing season. However, this study and previous studies relating differences in stem or leaf water potential to rootstock-induced vigor were limited in that they only showed correlations between differences in tree growth and plant water potential values. Subsequent research showed that the rate of stem extension growth could be directly altered in trees growing on both dwarfing and invigorating rootstocks through manipulating stem water potential by temporarily decreasing the exposed canopy volume (Solari et al. 2006a) or by root pressurization (Solari and DeJong 2006).

It is well-known that water stress can have dramatic negative effects on stomatal conductance that, in turn, can negatively affect photosynthetic rate, even though photosynthetic responses to dehydration are species specific (Kramer and Boyer 1995). Steinberg et al. (1989) reported that water stress significantly decreased net photosynthesis of peach trees via stomatal limitations. Solari et al. (2006a) and Solari and DeJong (2006) demonstrated that hydraulic limitations of the size-controlling peach K146-43 rootstock caused stomatal-limited photosynthesis in the scion. Therefore, it appears that the influence of size-controlling peach rootstocks on tree water relations affects tree growth not only by direct effects on the shoot extension growth rate, but also through indirect long-term influences due to a decreased net CO_2-exchange rate mediated by stomatal conductance limitations. Similarly, Gonçalves et al. (2006) reported that sweet cherry trees grafted on dwarfing rootstocks had lower stem water potentials, stomatal conductances, net CO_2-exchange rates, intercellular CO_2 concentrations, and maximum photochemical efficiencies of photosystem II than trees on invigorating rootstocks. However, data about the effects of size-controlling rootstocks on both stomatal conductance and net photosynthesis are inconsistent across different studies. Even though Olien and Lakso (1986) found that midday stem water potential increased progressively from dwarfing to more invigorating rootstocks, they did not find any relationship between stomatal conductance and stem water potential in apple trees grafted on rootstocks with differing vigor-controlling potentials. However, Cohen and Naor (2002) reported that lower midday shaded-leaf water potential of apple trees grafted on M.9 was associated with a lower midday canopy conductance compared to trees grafted on MM.106 (trees on the intermediate-vigor Hashabi rootstock had intermediate values of midday shaded-leaf water potential and canopy conductance).

The effect of dwarfing apple rootstocks on leaf photosynthesis also is not consistent in the literature. Brown et al. (1985) and Schechter et al. (1991) reported that leaf net CO_2-exchange rates of apple trees grafted on size-controlling rootstocks were significantly lower than on invigorating rootstocks, whereas Fallahi et al. (2001) reported that a statistically significant rootstock effect on net photosynthesis was not always related to rootstock vigor-controlling potential. However, Barden and Ferree (1979) concluded that rootstocks did not affect net leaf photosynthetic rate and leaf transpiration rate of one-year-old container-grown 'Delicious' apple trees. Similarly, Lliso et al. (2004) did not find any significant effect of dwarfing rootstocks on CO_2-exchange rate of 'Navelina' orange trees. This inconsistency of results regarding the effect of size-controlling apple rootstocks on photosynthesis and stomatal conductance makes it difficult to draw conclusions on the importance of these parameters in rootstock-induced dwarfism in apples.

Olien and Lakso (1984, 1986) performed indirect estimates of root hydraulic conductivity and suggested that low midday stem water potential induced by dwarfing rootstocks might be related to low hydraulic conductivity of the root system and/or the graft union. This hypothesis could explain the results of Hussein and McFarland (1994), who reported that during the development of water stress, sap flow in apple trees on dwarfing rootstock (MAC9) decreased faster than in trees on an invigorating rootstock (seedling). The hypothesis formulated by Olien and Lakso (1984, 1986) and others (Beakbane 1956) has support from anatomical studies of the conducting system of the rootstock and of the graft union. Early studies (Beakbane and Thompson 1939) found that dwarfing apple rootstocks had roots with fewer and smaller xylem vessels than invigorating rootstocks. McKenzie (1961) reported that the percentage of bark tissue and of wood ray tissue per unit of cross-sectional area in roots of apple trees grafted on M.9 was almost twice that of trees grafted on the very vigorous M.16 rootstock. In addition, as previously stated, several studies (Simons and Chu 1984; Simons 1986, 1987; Ussahatanonta and Simons 1988; Soumelidou et al. 1994a) have described morphological and developmental anomalies in the vascular system at the graft union of trees on dwarfing apple rootstocks. Thus, in some fruit trees on dwarfing rootstocks, the graft union may cause significant resistance to water flow (and also to transport of solutes and hormones) from the root system to the canopy.

Several researchers have studied the efficiency of root system and graft union for water transport in fruit trees grafted on vigor-controlling rootstocks, but the results are often species specific. In apple trees, hydraulic limitations of the root system and/or the graft union appear to play an important role in the rootstock-mediated dwarfing phenomena. Leaf-specific soil-to-stem hydraulic conductance was significantly lower in apple trees grafted on M.9 than trees on MM.106, whereas there was no significant rootstock effect when soil-to-stem hydraulic conductance was normalized by sapwood cross-sectional area (Cohen and Naor 2002). Thus, differences in stem water potential between trees on apple rootstocks with differing vigor-control potentials do not appear to be related to stem wood properties, but are more likely due to the inefficiency of the root system (plus graft union) in supplying water to the leaves, especially when climatic evaporative demand is high. However, Cohen and Naor (2002) analyzed the root-to-stem pathway as a whole and did not identify where the higher hydraulic resistances were located (e.g. in the root system, in the rootstock stem, in the graft union, or in all of these organs). Atkinson et al. (2001, 2003) measured the hydraulic conductivity of sections of apple tree stems that included a piece of scion stem, the graft union, and a piece of rootstock shank that were considered as three hydraulic resistances placed in series. They reported that hydraulic conductivity of the entire stem section (scion + graft union + rootstock) dramatically decreased from trees grafted on the vigorous MM.106 to trees on the semidwarfing M.9, and to trees on the dwarfing M.27, and that the progressively decreasing conductivity of the graft union tissues could account for most of these differences. These differences in hydraulic conductivity of the graft union between rootstocks were in agreement with the percentage of functional xylem area determined with safranin staining (the percentage of functional xylem area in the graft union decreased with increasing vigor control capacity of the rootstock). Bauerle et al. (2011) also reported that under well-watered conditions, hydraulic resistance of the graft union was significantly higher in apple trees on dwarfing rootstocks (B.9) compared to semidwarfing rootstocks (MM.111). Interestingly, Atkinson et al. (2003) reported that dwarfing rootstocks also induced a significant decrease in scion stem conductivity, even when conductivity was normalized by xylem cross-sectional area, indicating that size-controlling rootstocks may also have significant effects on anatomical features of the scion conducting system of apple trees. This result was supported by the progressively increasing percentage of functional xylem area in scion stems grafted on rootstocks with decreasing vigor-controlling capacity. In addition, hydraulic conductivity (even when normalized by root cross-sectional area) of individual roots (1–2 mm diameter) of ungrafted, dwarfing M.27 rootstock was 50% of that of ungrafted, vigorous MM.106 rootstocks (Atkinson et al. 2003). Even though this result was relative to only one root size class (1–2 mm diameter), it is in agreement with the hypothesis that dwarfing apple rootstocks have intrinsic anatomical characteristics that directly affect their hydraulic properties (Beakbane and Thompson 1939). In addition, Bauerle et al. (2011) reported that the plant response to drought in terms of decrease in xylem vessel diameter of apple trees on the dwarfing B.9 was less plastic compared to trees on the semidwarfing MM.111. The phloem-to-xylem ratio measured in roots with a diameter of 1.5–2.0 mm has been negatively correlated with root-specific sap flow (a measure of the ability of the root system to absorb and transport water) and with rootstock vigor (Iwanami et al. 2009). This is in agreement with the proposal that the phloem-to-xylem ratio may be useful as a tool for early screening of dwarfing rootstocks in apple-breeding programs more than a half-century ago (Beakbane and Thompson 1947). The possible implication of hydraulic resistance in the dwarfing mechanism of apple rootstocks is also supported by the fact that increasing grafting height or the length of an interstock increases the degree of the size-controlling effect (Parry and Rogers 1972; Parry 1986).

In peach trees, the water relations theory has been supported by several studies. Basile et al. (2003b) reported that leaf-specific conductance of the root system of trees on the size-controlling K146-44 rootstock was 22% lower than that of trees on the invigorating Nemaguard rootstock, but in peach there was no significant contribution of the graft union to the total resistance to water flow of the rootstock + graft union system. Basile et al. (2003b) also did not find any significant effect of the rootstock on leaf-specific scion conductance. These results were confirmed in later studies carried out with similar rootstocks (Solari et al. 2006b,c). In contrast to work with apple, these studies indicate that graft union hydraulic resistance does not play an important role in peaches when graft compatibility is not a problem. Peach trees grafted on size-controlling rootstocks partitioned greater proportions of dry matter to the root system compared to trees on Nemaguard (Basile et al. 2003b; Solari et al. 2006b); therefore, the greater hydraulic resistance associated with vigor-controlling rootstocks does not appear to be a function of differential dry matter partitioning between the root and scion. In fact, Solari et al. (2006b) reported a significant, positive, and linear relationship between the scion-to-rootstock dry mass ratio and rootstock-to-scion hydraulic conductance ratio across trees grafted on three rootstocks with differing size-controlling potentials. These relationships suggest peach trees grafted on size-controlling rootstocks partially compensate for the inefficiency of their root systems in supplying water to the scion by increasing the dry matter partitioning to the root system (in turn, this preferential dry matter partitioning to the root system may further decrease the growth of above-ground organs). However, this may not be the case for dwarfing rootstocks of apple. Lo Bianco et al. (2003) found that apple trees on the dwarfing M.9 had lower root-to-shoot ratios than trees on the vigorous MM.106.

It appears the high resistance to water flow of size-controlling peach rootstocks is due to intrinsic factors within the root system. Solari et al. (2006c) did not find any difference associated with peach rootstock vigor in the root branching pattern (as indicated by the number of root tips per unit dry weight). Basile et al. (2007) also did not find any relationship between the size-controlling potential of five peach rootstocks and the total amount or the seasonal pattern of fine root production per unit soil surface (both analyzed with a minirhizotron technique). However, Solari et al. (2006c) and Basile et al. (2007) found that peach trees grafted on the dwarfing K146-43 rootstock had thicker fine roots than more vigorous rootstocks. This is consistent with reports of negative correlations between root diameter and root conductivity across different *Prunus* species (Rieger and Litvin 1999) and that root-specific surface area (root surface per unit dry weight) was lower in low-vigor peach tree–rootstock combinations compared to trees on more vigorous rootstocks (Solari et al. 2006c). Syvertsen and Graham (1985) also correlated this parameter with differences in root hydraulic conductance between rootstocks of citrus trees. Rodríguez-Gamir et al. (2010) also reported that citrus rootstocks with low root hydraulic conductivity had larger hypodermal cells in fibrous roots and suggested that this could account for some of this reduced conductivity. Basile et al. (2007) found a negative relationship between rootstock vigor and specific root length of roots produced in spring, and this suggests that peach trees grafted on rootstocks with differing size-controlling potentials may follow different strategies when building new fine roots in spring. Trees on rootstock of low-intermediate vigor tended to invest less carbon per unit length of root produced in spring compared with trees on more vigorous rootstocks; however, specific root length of roots produced in summer and fall was unrelated to rootstock vigor.

Although some evidence suggests that differences between peach rootstocks with differing vigor in hydraulic resistance may occur in the radial pathway in the absorbing roots, a recent study (Tombesi et al. 2010a) demonstrated that the diameter of xylem vessels progressively decreased from a vigorous peach rootstock (Nemaguard) to an intermediate-vigor rootstock (Hiawatha) and a dwarfing rootstock (K146-43). In addition, the density of vessels was also lower in Hiawatha and K146-43 compared to Nemaguard. These differences resulted in significant differences in theoretical axial xylem conductance (calculated with

Hagen-Poisseuille's law) that progressively decreased with decreasing rootstock vigor. This appears to account for the differences between these rootstocks in hydraulic conductance directly measured in previous studies (Basile et al. 2003b; Solari et al. 2006b,c). The good relationship between rootstock vigor and xylem anatomical characteristics (and calculated axial xylem conductance) was confirmed using a different set of peach rootstocks with differing size-controlling potentials (Tombesi et al. 2011). In addition, Tombesi et al. (2010b) reported that with peaches the dwarfing genotypes, when used as rootstock or interstock, do not significantly affect the xylem anatomy of the scion or the rootstock (when used as a dwarfing interstock). This suggests that most of the dwarfing mechanism is genetically controlled and is limited to the specific part of the tree consisting of the dwarfing genotype. These results suggested that anatomical features (xylem anatomy) may be useful as a tool for early selection of potential dwarfing peach rootstocks in breeding programs (Tombesi et al. 2011; Bruckner and DeJong 2014).

Similar results to those described for peaches have been reported for citrus rootstocks by Syvertsen (1981). Citrus trees grafted on the size-controlling 'Cleopatra' mandarin and sour orange rootstocks had lower root hydraulic conductivity than trees on the relatively more vigorous 'Carrizo' citrange and rough lemon rootstocks. These differences appear to be in agreement with the findings of Vasconcellos and Castle (1994), who reported that xylem vessel densities and diameters in grapefruit trees on 'Cleopatra' mandarin and sour orange rootstocks were less than in trees on 'Carrizo' citrange and rough lemon. Recently, Rodríguez-Gamir et al. (2010) provided additional evidence that differences in root hydraulic conductivity between citrus rootstocks can be explained by differences in the diameter of xylem vessels. Differences in root hydraulic conductivity between citrus trees on rootstocks with differing vigor-controlling potentials appeared to be positively correlated with root-to-shoot ratio, whole-tree transpiration, maximum rates of net CO_2, and water-vapor leaf exchange rates (Syvertsen and Graham 1985).

Nardini et al. (2006) compared the water relations of olive trees grafted on the vigorous 'Leccino Minerva' and the dwarfing 'Leccino Dwarf' rootstocks. They reported that the rootstock did not significantly affect the linear relationship between root hydraulic conductance and total-tree leaf area. Thus, trees on the two rootstocks had comparable root leaf-specific hydraulic conductance. The absence of differences between rootstocks in root leaf-specific hydraulic conductance resulted in no differences in leaf water potential and, in turn, leaf transpiration rate. In spite of these results, the authors, in their discussion, maintained that hydraulic limitation may play an important role in rootstock-mediated dwarfism in olive trees since a reduction in leaf-specific hydraulic conductance is not a necessary condition to have hydraulic limitation occur. For instance, it has been reported in *Pinus palustris* that changes in hydraulic architecture may result in reduced growth even if leaf-specific hydraulic conductance, leaf water potential, and stomatal conductance are not affected (Addington et al. 2006). Therefore, Nardini et al. (2006) proposed that olive scions grafted on dwarfing rootstocks slow down their growth to compensate for a change in hydraulic architecture induced by the rootstock in order to maintain homeostasis in leaf water potential and gas exchange. In a follow-up study (Trifilò et al. 2007), 'Leccino Dwarf' rootstock induced the production of narrow, short xylem conduits in the scion ('Leccino Minerva') compared to self-rooted 'Leccino Minerva' roots, but, at the same time, the 'Leccino Dwarf' roots induced a 25% increase in vessel density (number of xylem conduits per unit wood cross-sectional area) in scion shoots compared to self-rooted 'Leccino Minerva' trees. These two rootstock effects on vessel density and vessel diameter appeared to compensate for each other, and thus the rootstock did not appear to affect the potential capacity of the wood to supply leaves with water. In another study, Gascó et al. (2007) reported that hydraulic resistance of the graft union in adult olive trees grafted on dwarfing rootstocks does not play an important role in dwarfing mechanisms, similar to reports for peach (Basile et al. 2003b; Solari et al. 2006b).

Gonçalves et al. (2007) reported that the root system of sweet cherry rootstocks (GiSelA 5) had xylem vessels and xylem-to-phloem thickness ratios that were significantly smaller than those of invigorating rootstocks, and this may decrease axial hydraulic conductance of the root system of dwarfing cherry rootstocks. These results are similar to those from previous studies on apple rootstocks (Beakbane and Thompson 1939). Olmstead et al. (2006a,b) reported that both in the graft union and in the scion of sweet cherry trees grafted on dwarfing rootstock (GiSelA 5), there were smaller, fewer, and irregularly orientated xylem vessels compared to those in vigorous cultivar–rootstock combinations. These results were supported by the findings of Meland et al. (2007).

Clearwater et al. (2004) reported that kiwifruit vines on dwarfing rootstocks had higher soil-to-stem hydraulic conductance than vines on an invigorating rootstock. Also, the graft union did not appear to limit hydraulic conductance of kiwifruit vines on size-controlling rootstocks (Clearwater et al. 2004). However, a delay of several weeks after budburst in the accumulation of root pressure in dwarfing compared with vigorous kiwifruit rootstocks was observed (Clearwater et al. 2007). This was in agreement with previous research (Clearwater et al. 2006) indicating that most of the effects of size-controlling rootstocks on scion development in kiwifruit occur early in the growing season immediately after bud-break and that rootstock effects in kiwifruit were associated with how early the rootstock genotypes became active in comparison with bud-break of the scion.

An aspect of the hydraulic conductance–vessel diameter or number aspect of the water relations theory that needs to be specifically addressed is: how can rootstock xylem hydraulic conductance be limiting when the volume of xylem sapwood appears to be in excess of what is needed to meet the transpirational demands of the tree? In other words, where did Rogers and Beakbane (1957) go wrong with their conclusion that xylem was not a growth-limiting factor in dwarfing rootstocks (DeJong et al. 2013)? Beakbane and his colleagues never made a clear functional link between rootstock xylem anatomical characteristics and the vigor that rootstocks impart to scions because the prevailing view at the time was that xylem vessels were in substantial excess compared to what was necessary to efficiently move water through the plant (Preston 1952; Rogers and Beakbane 1957). However, it is now known that the majority of water movement through the xylem in species with ring-porous xylem anatomy occurs in the most recent ring of xylem, and older rings of xylem are often nearly nonfunctional for conducting water up the tree (Ellmore and Ewers 1985, 1986). In a recent study, Tombesi et al. (2014) showed that branch-girdling peach trees in spring temporarily decreases stem water potential until the girdle heals, presumably because girdling interrupts early-spring xylem development and thus branch hydraulic conductivity. This study documented that hydraulic conductance can indeed be limiting in spring, even though several rings of active sapwood appear to be present. Clearly, not all sapwood is equally capable of conducting water, and efficient water transport in the spring appears to depend highly on newly formed xylem.

C. The Nutritional Theory

According to the nutritional theory, dwarfing rootstocks control fruit tree size by inducing nutritional deficiencies in the scion. It is generally envisioned that this could happen in a similar manner as has been described for the water relations theory (i.e. either the rootstock is not as efficient at uptake and delivery of nutrients to the scion, or the graft union represents an impediment to the transport of nutrients to the scion) (Figure 2.1.) Support for this theory is not as plentiful as for some of the other theories, but it is substantial (Table 2.3). Several studies have reported that tree nutritional status was correlated to size-controlling potential of the rootstocks (Boyhan et al. 1995; Neilsen and Kappel 1996; Rosati et al. 1997; Fallahi et al. 2001; Moreno et al. 2001; Zarrouk et al. 2005; Thorp et al. 2007; Neilsen and Hampson 2014). The hypothesis that size-controlling rootstocks have lower capacity in nutrient uptake was supported by an early study of Bukovac et al. (1958), who reported that own-rooted cuttings of M.7 and M.9 absorbed less ^{32}P than cuttings of M.16 and 'Delicious' seedlings. Similar patterns were obtained when the authors compared ^{32}P and ^{45}Ca uptake of 'McIntosh' apple grafted on invigorating and dwarfing rootstocks. In addition, their results appeared to exclude the role of the graft union resistance in nutrient transport to the scion, because they did not find any significant accumulation of ^{32}P and ^{45}Ca at the graft union. Ruck and Bolas (1956) measured the net assimilation rate of a vigorous (Crab C) and a dwarfing (M.9) rootstock grown in sand culture under four different levels of nitrogen application (5, 17, 58, and 200 ppm): the net assimilation rate was always higher in Crab C than in M.9, and the differences increased dramatically under conditions of limited nitrogen supply. Zhu et al. (1999) made all possible reciprocal graft combinations of own-rooted M.26 (a semidwarfing rootstock) and 'Gravenstein' (a vigorous apple cultivar), and grew trees under limiting and nonlimiting nitrogen supply. Their results suggested that the dwarfing mechanism is related to morphological characteristics of the root system that can directly affect nutrient uptake capacity (specific root length and total root length).

The graft union of apple trees on dwarfing rootstocks also has been reported to deplete nutrients during sap flow across the union. For instance, Jones (1971, 1976, 1984) correlated the dwarfing effect of apple rootstocks and interstocks to a lower solute concentration in the sap collected above the graft union compared to that extracted below the graft union. However, Webster (2004) expressed doubts about this hypothesis based on unpublished data collected at the East Malling experimental station by Else. According to Webster (2004), these types of experiments demonstrated that the depletion of nutrient in the sap by the graft union of trees on dwarfing rootstocks occurred only when measurements are made with low sap flow rates, whereas nutrient depletion did not occur at flow rates typical of tree transpiration. Recent studies by Else (M.A. Else, unpublished) in which sap flow rates were controlled have confirmed Webster's (2004) assertion. In the literature, the relationship between tree nutritional status and size-controlling potential of the rootstock is often very inconsistent. Indeed, several studies have reported that the relationship between these two parameters was not clear (Simons and Swiader 1985). Webster (2004) assigned the inconsistency of these results potentially to the different genera, species, cultivars, tree ages, and methodological problems involved in the studies.

D. The Hormonal/Signaling Theory

Growth of above and below-ground organs of fruit trees are thought to be coordinated and influence each other following complex cyclic patterns of feedbacks (Costes et al. 2006). The hormonal theory of size control is based on the assumption that plant hormones represent endogenous, organ-to-organ, long-distance signals (shoot-to-root and root-to-shoot) that fine-tune and coordinate growth of the root system and above-ground organs (Figure 2.2). This conceptual framework is strictly connected with the "hormone message concept" of plant

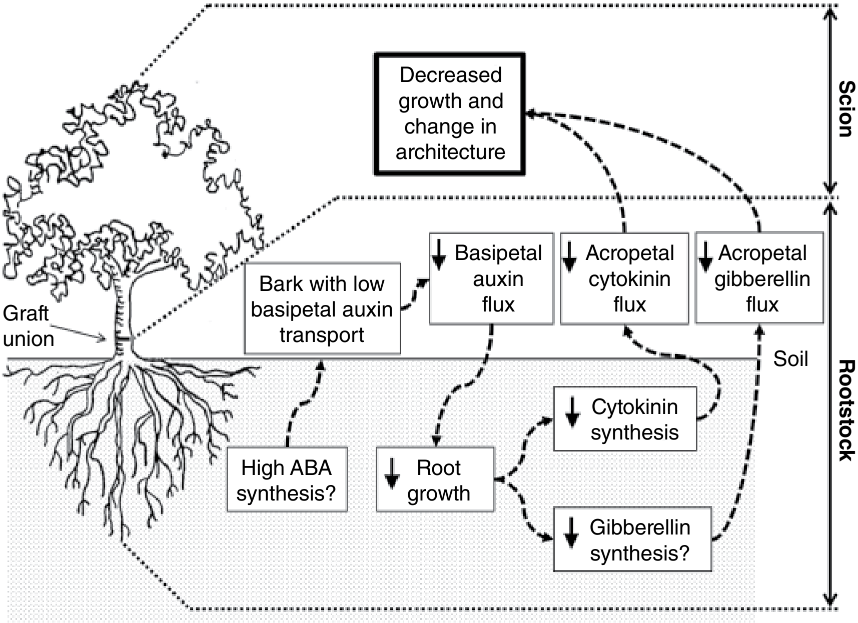

Figure 2.2 Schematic diagram for describing possible interactions between the rootstock and scion with regard to long-distance hormone transport/signaling theories concerning dwarfing rootstocks.

development, according to which hormones produced in one part of the plant are transported to their site of action where they influence growth (Jackson 1993). This theory is well represented in research reports (Table 2.3), has received a lot of attention in traditional pomology literature, and has been recently reviewed (Aloni et al. 2010). It is well known that hormones exert control on physiological phenomena like apical dominance (Dun et al. 2006; Müller and Leyser 2011). In various fruit tree species, size-controlling rootstocks appear to decrease the sylleptic growth (Cook et al. 2004; van Hooijdonk et al. 2010; A.M. Weibel, EEA Junín, INTA, Argentina, personal communication) compared to invigorating rootstocks, and this supports the hypothesis that rootstocks with differing vigor-controlling potentials may modify the hormonal relationships within fruit trees.

Lockard and Schneider (1981) promoted the hormonal theory based on the action of two types of hormones: auxins and cytokinins. Auxins are synthesized in leaf primordia and young leaves, and are transported basipetally to roots both by mass-flow in mature phloem and by much slower, carrier-dependent, cell-to-cell, polar transport (through the vascular cambium, differentiating xylem vessels, and differentiating xylem parenchyma) (Morris et al. 2004). Cytokinins are synthesized in root tips and transported acropetally from root to shoot via the xylem (Davies 2004). It is thought that auxins stimulate root initiation and cytokinins stimulate cell division, shoot growth, and leaf expansion (Davies 2004). Jones (1973) provided experimental evidence that root-synthesized cytokinins are essential for shoot growth of apple trees. There is much experimental evidence supporting the role played by auxins and cytokinins in influencing the root-to-shoot ratio in plants and in restoring it after an external disturbance (Beck 1996; Vysotskaya et al. 2001). According to Lockard and Schneider (1981), the amount of active auxin that reaches the root systems has direct effects on root growth, metabolism, and also cytokinin biosynthesis. Similarly, the amount of cytokinins reaching the shoot is thought to directly affect shoot growth and, in turn, the amount of auxins synthesized and translocated to roots. Based on this framework, Lockard and Schneider (1981) hypothesized that dwarfing apple rootstocks were characterized by bark with a lower capacity for auxin transport than invigorating rootstocks. They hypothesized that the small amounts of auxins reaching the root system of dwarfing rootstocks would affect root growth, cytokinin production, and, consequently, shoot growth. Previously, Gur and Samish (1968) reported that the amount of auxins catabolized by the bark was higher in dwarfing rootstocks than in invigorating rootstocks. According to these findings, decreased auxin flux toward the root system of dwarfing rootstocks may be caused by the higher auxin catabolism rates occurring in the bark of size-controlling rootstocks instead of by lower bark auxin transport capacities, compared to the invigorating rootstocks (as suggested by Lockard and Schneider 1981).

The Lockard and Schneider (1981) hypothesis was supported by earlier studies that demonstrated that grafting a ring of bark from a dwarfing rootstock onto an apple tree induced dwarfism in a tree composed of a vigorous cultivar–rootstock combination, just as if the rootstock was used as an interstock (Lockard and Schneider 1981). Similar results were obtained when a ring of bark from the scion of a vigorous cultivar–rootstock combination was removed and regrafted on the same tree but with inverted polarity (Lockard and Schneider 1981). It has also been noted that the size-controlling effect of apple dwarfing rootstocks is stronger when grafting height or the length of an interstock is increased (Parry and Rogers 1972; Parry 1986). These findings appear to support the hypothesis that bark tissue is the organ where most of the mechanism of rootstock-mediated vigor control of apple trees occurs. Also in support of this hypothesis, Harrison et al. (2016) have proposed a three-locus genetic model for rootstock-induced dwarfing in apple through genetic mapping of the percentage of the cross-sectional area of roots consisting of root cortex.

However, Lockard and Schneider (1981) also stated that not all the experimental results obtained in their studies could be explained completely with their hormonal theory. Furthermore, in some stone fruit species, if size-controlling rootstocks are used as interstocks, they do not induce the same vigor control in the scion, and this suggests that, perhaps for stone fruit species, bark is not the tree organ necessary for a dwarfing effect to occur (Webster 2004).

Subsequent studies have provided evidence that trees on M.9 dwarfing apple rootstock have lower basipetal auxin transport in apical shoots (Soumelidou et al. 1994b; Kamboj et al. 1997a,b) and from scion leaves to roots (Kamboj et al. 1997a) than vigor-inducing rootstocks. Kamboj et al. (1999a) also reported that cytokinin concentration in root pressure exudate and in shoot xylem sap was lower in dwarfing apple rootstocks than in invigorating rootstocks. Similarly, Skene and Antcliff (1972) reported that ‘Sultana’ grapevines grafted on the vigor-controlling 1613 rootstock had lower amounts of cytokinins passing from roots to shoot compared to self-rooted vines and vines grafted on the invigorating ‘Salt Creek’ rootstock. Orange trees grafted on the invigorating ‘Volkamer’ lemon rootstock also have higher cytokinin-like activity in branch sap than trees on the less vigorous ‘Troyer’ (*Poncirus trifoliata* × *Citrus sinensis*) rootstock (Saidha et al. 1983). Sorce et al. (2002)

also reported that in both grafted and ungrafted peach trees, tree vigor was positively correlated with the cytokinin transport rate in the xylem.

If endogenous cytokinins are the primary root-to-shoot hormone signal involved in the dwarfing mechanism, then it would be expected that exogenous application of cytokinins to scions grafted on dwarfing rootstocks should resume growth, canceling the differences in vigor with trees grafted on vigorous rootstocks. However, exogenous applications of benzylaminopurine (BAP or BA) to apple scions on dwarfing rootstocks either did not increase (Wertheim and Estabrooks 1994) or decrease (van Hooijdonk et al. 2010) primary shoot growth, but did stimulate sylleptic branching (Kender and Carpenter 1972; van Hooijdonk et al. 2010). A change in architecture can explain only part of the dwarfing phenomenon, and for this reason other hormones have been hypothesized to be involved. Gibberellins are synthetized in growing tissues and have important functions in stem extension growth (Davies 2004; Yamaguchi 2008). Evidence of the role of gibberellins in shoot growth has been provided by Bulley et al. (2005), who reported that ‘Greensleeves’ apple scions transformed to downregulate the expression of a GA 20-oxidase gene (a gene involved in gibberellin synthesis) were dwarfed, even though the transformed cultivar was grafted onto vigorous rootstocks (M.25 and MM.106).

Gibberellins or gibberellin-like substances are present in the xylem sap (Motosugi et al. 1996), and for this reason it has been hypothesized that some gibberellins and/or their precursors are synthetized in the root system and then transported in the xylem to the shoot, where they can be metabolized to produce bioactive gibberellins (Dodd 2005; Yamaguchi 2008). The possible involvement of gibberellins in rootstock-induced dwarfing was supported by early apple studies. Concentrations of some gibberellin-like substances were lower in the roots, shoots, and leaves of ungrafted plants of M.9 compared to MM.111 (Yadava and Lockard 1977). Similarly, there is some evidence that M.9 interstocks have lower capacity for transporting gibberellin-like substances to the scion compared to the vigorous MM.115 interstock (Richards et al. 1986). These results appear to give support to the findings of a previous study from Ibrahim and Dana (1971), who found that the concentration of gibberellin-like substances in the xylem sap collected above the graft union was significantly lower in ‘Golden Delicious’ trees grafted on M.9 compared to trees on M.1.

Recently, in a comprehensive study testing the hormonal theory, Van Hooijdonk et al. (2010) designed an experiment to study the role of auxins, cytokinins, and gibberellins in the dwarfing induced by apple rootstocks. Their results suggest that the three hormone families play a role in growth responses on dwarfing rootstocks, supporting the hypothesis that auxins are basipetally transported from the scion to the rootstock and affect root growth, while the amount of cytokinins and gibberellins produced in the roots and transported to the shoots affect shoot growth. In addition, the same study reported that cytokinins mainly stimulated sylleptic branching, whereas gibberellins increased shoot growth mainly by prolonging the season for new node production. However, in this paper, M.9 significantly decreased the number of nodes of the primary shoot at the end of the first vegetative season after grafting, whereas the same authors in a following study with the same dwarfing rootstock (Van Hooijdonk et al. 2011) did not find this effect to be significant. Literature about the effect of M.9 on primary shoot length during the first growing season after grafting is often contradictory, and this increases the complexity of interpreting the role of these hormones in the dwarfing phenomenon.

In addition to auxins, cytokinins, and gibberellins, abscisic acid is reported to play a role in rootstock-induced dwarfism in fruit trees. In an early study, the concentrations of abscisic acid–like substances were reported to be higher in the roots, shoots, and leaves of ungrafted plants of M.9 compared to MM.111 (Yadava and Lockard 1977). More recently, Kamboj et al. (1999b) reported that shoot bark of dwarfing rootstocks had higher concentrations of abscisic acid (and higher abscisic acid–indoleacetic acid ratios) than other vigorous rootstocks and speculated that abscisic acid may have an important role in reducing polar auxin transport, as is suggested to occur in beans (Basler and McBride 1977). Similar results were found in ‘Eureka’ lemon trees grafted on the dwarfing Flying Dragon rootstock compared to the invigorating Swingle citrumelo rootstock (Noda et al. 2000). In contrast, Feucht et al. (1974) did not find any difference in abscisic acid concentration in shoot bark and cambial tissues between three *Prunus* species with differing vigor (standard-sized *P. avium*, medium-vigor *P. cerasus*, and dwarfing *P. cerasus*).

Recent studies have demonstrated that other compounds such as proteins and mRNAs are transported over long distances within plants, and they are considered to play an important role as signals in growth regulation (Lough and Lucas 2006; Atkins et al. 2011). Transport has also been reported to occur across the graft union (rootstock-to-scion long-distance transport and vice versa) in many plant species (Harada 2010), including fruit trees (Kanehira et al. 2010). Recent studies have demonstrated that dwarfing rootstocks can modify gene expression in the scion in apples (Jensen et al. 2003, 2010) and cherries (Prassinos et al. 2009). Rootstock-regulated gene expression in apple scions appears to start as early as six weeks after grafting (Jensen et al. 2010). A number of candidate transcripts have been indicated to be possibly involved in the dwarfing mechanism induced by apple rootstocks. For instance, Jensen et al. (2010) reported that APPLE0F000059320 transcript, which is thought to encode for sorbitol dehydrogenase (SDH), was expressed at higher levels in 'Gala' apple trees grafted on vigorous rootstocks compared to weak rootstocks. They suggested that this transcript explained 34% of the difference in tree vigor induced by the rootstocks. Since sorbitol is the main compound that many fruit trees in the *Rosaceae* (apples, pears, peaches, cherries, plums, and apricots) use to transport carbon from source to sink organs, and since SDH converts sorbitol to fructose in sink organs (Loescher 1987), Jensen et al. (2010) suggested that shoot tips of trees on vigorous rootstocks are more active carbohydrate sinks. Prassinos et al. (2009) reported that cherry trees on rootstocks with different vigor were characterized by differences in the timing of shoot growth cessation, and these differences were associated with significant differential temporal patterns of gene expression. The same authors suggested several candidate genes that can be putatively involved in the dwarfing mechanism. Some of these genes were also reported to be differentially expressed in apple trees grafted on rootstocks with different vigor (Jensen et al. 2003).

Along similar lines, Foster et al. (2014) suggested that upregulation of a suite of flowering genes, including *MdFT* and possibly *MdBFT*, in the vasculature of M.9 apple rootstocks may be part of the underlying mechanism of apple dwarfing rootstocks. Genes involved with responses to biotic and abiotic stress were also upregulated in the M.9 rootstock, suggesting that stress, possibly mediated by jasmonic acid and ABA signaling, could also play a role in the M.9-related dwarfing response. The hormone theory has recently been further complicated by Zhang et al. (2015), who have proposed that dwarfing mechanisms in apple differ with cultivars involved in scion–rootstock or scion–interstem–rootstock combinations. They hypothesized that the dwarfing effect in 'Fuji'/M.9 is related to weak zeatin (cytokinin-type substance) synthesis in the roots of M.9, whereas in the 'Fuji'/M.9/Baleng Crab combination, the dwarfing effect was induced by lower expression of the *MdPIN8* gene in the M.9 interstem bark, which limited IAA basipetal transport and root IAA supply and in turn inhibited root zeatin biosynthesis. In both cases, they suggested that weak zeatin synthesis in the roots contributed to moderate zeatin deficiency in the shoots that inhibited vegetative growth of those shoots.

Pernice et al. (2006) tested the hormonal/signaling theory in peach trees grafted on size-controlling rootstocks that, in other studies, have been demonstrated to control tree vigor by modifying tree water relations (Basile et al. 2003a,b; Solari and DeJong 2006; Solari et al. 2006a,b,c; Tombesi et al. 2010a). Pernice et al. (2006) imposed a drastic decrease in canopy shoot-to-root ratio by severely pruning tree canopies just prior to bud-break. The authors hypothesized that if hormones played a substantial role in the dwarfing mechanism induced by the group of peach rootstocks studied, differences in shoot growth between trees on the different rootstocks would appear even when differences in water status were artificially annulled. Instead, the severe pruning treatment negated rootstock-induced differences in extension growth rates of individual shoots during the postpruning spring growth flush, indicating no apparent intrinsic differential hormonal control among the peach rootstocks used in the study.

Lliso et al. (2004) also tested the hormonal/signaling theory in orange trees on rootstocks with differing vigor-controlling potentials both by measuring the concentration of different gibberellins in summer sprouts and by applying exogenous hormones (6-benzyladenine, gibberellic acid, and indoleacetic acid) to latent buds. Their results did not appear to support any important involvement of hormones in the dwarfing mechanism of the citrus rootstocks involved in the study.

There is, therefore, general agreement that hormones and endogenous signals play a large part in the coordination of plant growth, and there is evidence that concentrations of hormones and signals appear to vary depending on scion and rootstock vigor. However, as with many hormone- and/or signal-based theories related to plant growth and development, it is very difficult to assign causality because if vigor of the scion is increased or decreased by another factor, changes in hormone/signal concentrations or transport as a result of the change in vigor would be expected. Thus, correlations between changes in scion vigor and changes in hormone concentration or transport do not imply causality unless manipulation of hormones can be used to reverse the response, and evidence for this is equivocal with rootstock-induced dwarfing.

E. The Carbohydrate Reserve Theory

The carbohydrate reserve theory suggests that differences in either carbohydrate reserve storage or mobilization capacity could vary among rootstocks or scion–rootstock combinations, such that the spring flush of growth is diminished when trees are growing on dwarfing rootstocks (Figure 2.3). This potential mechanism has received little attention among researchers (Table 2.3), even though the importance of storage

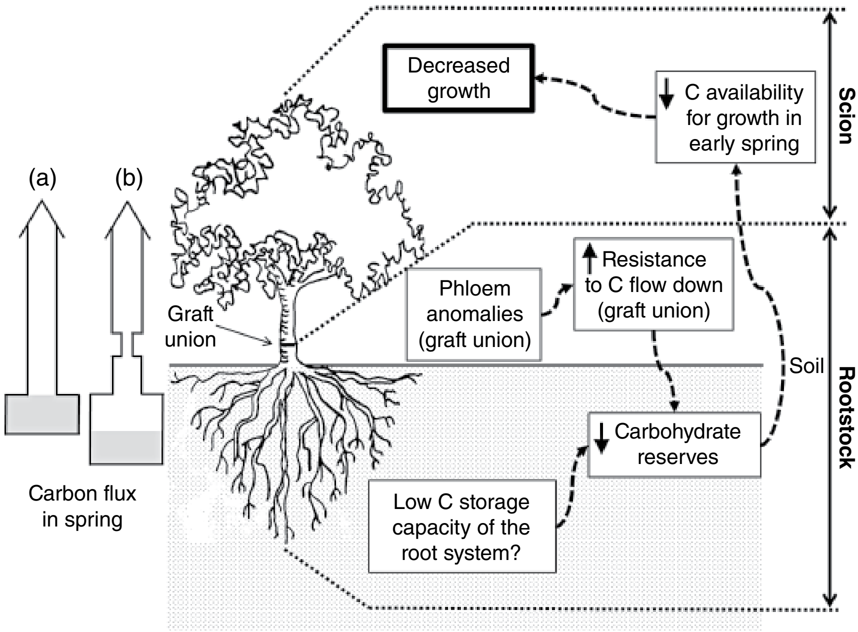

Figure 2.3 Schematic of carbohydrate storage–mediated size-controlling mechanisms for trees grafted on dwarfing rootstocks. The arrows on the left indicate that rootstocks may have a limited capacity to store carbohydrates (a) or the root storage capacity is not filled because of restricted flow of carbohydrates at the graft union (b).

reserves on supporting spring growth is well known (Priestley 1970; Loescher et al. 1990). This theory is based on the observation that most of the effect of dwarfing rootstocks on shoot growth occurs early in the growing season, when tree growth depends on stored reserves (Basile et al. 2003a; Weibel et al. 2003; Clearwater et al. 2006).

In deciduous fruit trees, shoot growth early in the season is supported by mobilizing carbohydrate reserves (mainly starch stored in the trunk and root system) at least until enough leaf area is developed to supply photosynthates to support growth (Murneek 1942; Loescher et al. 1990). Root carbohydrate reserves are generally accumulated during late summer and fall through long-distance shoot-to-root phloem transport, whereas in spring, starch is quickly hydrolyzed, and part of the available soluble carbohydrates is mobilized via the xylem back to the aboveground part of the tree to growing meristems (Priestley 1970; Loescher et al. 1990). Any factor hindering carbohydrate accumulation in storage organs (defoliation, shading, etc.) can have negative effects on vegetative growth early in the following season (Mika 1986; Loescher et al.

1990; Nzima et al. 1999). Since the root system is a major carbohydrate storage organ in fruit trees (Murneek 1942; Loescher et al. 1990), one possible hypothesis to explain the dwarfing mechanism is that size-reducing rootstocks are less efficient in accumulating root carbohydrate reserves and/or in remobilizing them. This hypothesis found recent support in the data published by Olmstead et al. (2010), indicating that total starch concentration was significantly lower in the root system of trees grafted on dwarfing rootstocks than on vigorous rootstocks. Weibel et al. (2011) also reported similar results on total nonstructural carbohydrate concentrations in peach size-reducing rootstocks. Several factors can be hypothesized to be involved in determining a smaller carbohydrate storage pool in the root systems of trees on dwarfing rootstocks. These include a limitation in the capacity of these trees for (i) assimilating CO_2, (ii) transporting carbohydrates from shoots to roots, or (iii) storing carbohydrates in the root system. Any combination of these factors could be involved.

The section describing the “water relations theory” cited papers indicating that dwarfing rootstocks can cause significant decreases in net CO_2-exchange rates in peach (Solari and DeJong 2006; Solari et al. 2006a) and cherry (Gonçalves et al. 2006) trees, whereas the reports about these effects are less consistent in apples (Barden and Ferree 1979; Brown et al. 1985; Schechter et al. 1991; Fallahi et al. 2001). Independent of the significance of effect of dwarfing rootstocks on photosynthetic rate per unit leaf area, trees with small canopies are expected to have lower total-tree CO_2 assimilation rates and less total-tree storage tissue (and therefore smaller storage carbohydrate pools) than vigorous trees. This can be further compounded by the effects of crop load on storage carbohydrates, since high crop loads can directly decrease carbohydrates available for storage and decrease the development of storage tissue and thus the storage sink (DeJong 2016).

Another possible hypothesis is that the graft union can be a zone of increased resistance for carbohydrate movement, limit carbohydrate transport from the scion to the rootstock, and cause sugar accumulation above the union. This hypothesis is consistent with the findings that trees grafted on dwarfing rootstocks can have morphological and developmental anomalies in the phloem at the graft union (Simons and Chu 1984; Simons 1986, 1987; Ussahatanonta and Simons 1988). Cherry trees grafted on the dwarfing GiSeLa 5 had lower starch concentration in the root system compared to trees on a vigorous rootstock, and total soluble sugar in the smaller trees tended to accumulate above the graft union (Olmstead et al. 2010). There is also clear evidence that the graft union can hinder carbohydrate transport in incompatible peach–plum grafts (Breen 1975; Moing et al. 1987; Moing and Gaudillère 1992). The involvement of alterations in carbohydrate metabolism in incompatible graft combinations is supported by a report that the UDP-glucose pyrophosphorylase (UGPase) transcript and its activity (playing a key role in interconversions between starch and sucrose) were lower in apricot–plum incompatible combinations than in compatible combinations (Pina and Errea 2008). Although we know of no studies that document that similar factors may be associated with the commonly observed overgrowth of many apple cultivars on M.9 dwarfing rootstock, this may be worthy of further study. Recent research with pears growing on dwarfing quince (*C. oblonga*) rootstock indicates that root carbohydrate concentrations were very low (<3.0% dry weight) throughout the year (J. Marsal, IRTA, Spain, personal communication), indicating that low carbohydrate storage may be involved in the dwarfing response caused by this rootstock.

A third possible mechanism that could account for the lower carbohydrate concentration in the roots of trees on dwarfing rootstock is that these rootstocks could have a genetically determined low carbohydrate storage capacity due to decreased relative amounts of storage tissue (mainly phloem and xylem parenchyma cells and xylem ray cells) and/or low storage capacity of these parenchyma cells. Carbohydrate storage is often considered to be a passive sink for carbohydrate (Le Roux et al. 2001). This means that only the carbohydrates that remain unused after satisfying the demand for seasonal maintenance, growth, and reproduction are stored. According to this concept, trees on dwarfing rootstocks that have a lower capacity for growth should be easily saturated with storage carbohydrates. However, in light of the importance of storage carbohydrates for survival of trees over successive years, it is more likely that carbon storage is an active sink competing with other organs for carbohydrates (Cannell and Dewar 1994; Silpi et al. 2007; Da Silva et al. 2014). According to this concept, there may be genotypic differences in the carbohydrate storage capacity of rootstocks that vary according to sink strength and capacity of root storage parenchyma cells, which thus influence the growth of the scion during spring carbohydrate mobilization. Select peach rootstocks have been reported to have root storage carbohydrate concentrations that vary in correspondence with their vigor (Weibel et al. 2011), but this does not appear to be a general phenomenon in many fruit tree species.

Recently, researchers working with the Malling series of dwarfing apple rootstocks have linked aspects of hormonal theory and carbohydrate theory to explain the dwarfing phenomenon. They have hypothesized that downregulation of auxin influx transporters reduces polar auxin transport in dwarfing rootstocks, and this is linked to reduced starch hydrolysis and sugar depletion during spring growth. This carbohydrate depletion subsequently leads to early termination of primary axis and sylleptic shoot growth of the scion (Foster et al. 2017).

The timing of carbohydrate mobilization in spring could also have some effect on the vigor of growth at that time. The vigor of kiwifruit vines growing on different rootstocks has been correlated with the timing of the development of root pressure associated with the rootstocks (Clearwater et al. 2007). Since root pressure is caused by the mobilization and secretion of soluble carbohydrates into xylem vessels, it is apparent that this type of growth stimulation or inhibition is likely to be a function of timing of root carbohydrate mobilization. While this is probably not a common mechanism involved with dwarfing rootstocks, it may deserve some attention since the chilling requirement of rootstocks is known to have effects on the growth of the scion in some species (Malcolm et al. 2011).

F. The Competition/Architecture Theory

This theory is based on the assumption that the final growth of each organ of a fruit tree is the result of a complex network of competitions between each growing organ, and different rootstocks can affect the balance of this competition. It is not as common or specific as some of the other theories (Table 2.3) but is worthy of mention. Based on the "source–sink" theory, trees have been described as collections of semi-autonomous but interacting organs whose carbon partitioning is driven by competition based on their growth potential, their proximity to source organs, and carbohydrate availability (Grossman and DeJong 1994; DeJong 1999; Allen et al. 2005). Fruit are considered the strongest sink for carbohydrates (Kramer and Kozlowski 1979), and the presence of fruit on the tree has been reported to depress shoot (Avery 1969; Grossman and DeJong 1995), trunk (Grossman and DeJong 1995; Intrigliolo and Castel 2007), and root growth (Heim et al. 1979; Williamson and Coston 1989; Basile et al. 2007). Several studies have demonstrated that some dwarfing rootstocks increase precocity of cropping in apples (Webster and Hollands 1999), cherries (Whiting et al. 2005), peaches (Loreti and Massai 1998), and pears (Jacob 1998). In addition, several studies have reported that dwarfing rootstocks can affect carbon partitioning between vegetative and reproductive growth in favor of the latter (Caruso et al. 1997; Inglese et al. 2002), and this effect is often measured as a higher yield efficiency (crop production per trunk cross-sectional area) of trees on size-controlling rootstocks than on invigorating rootstocks (Forshey and McKee 1970; Webster and Hollands 1999; DeJong et al. 2004). Furthermore, dwarfing rootstocks have been reported to increase fertility of adult trees by affecting flower induction. For instance, Kappel and Lichou (1994) reported that 'Burlat' sweet cherry trees grafted on the size-controlling Edabriz rootstock had more flowers per shoot length, more spurs per shoot length, and more flowers per spur compared to trees on the invigorating F12/1 rootstock. Between the second and the seventh growing seasons, 'Fuji' apple trees grafted on the dwarfing MAC9 had a higher flower bud density (number of flower buds per branch cross-sectional area unit) than trees on M.26 and MM.106 (Tustin et al. 2001). Similarly, shoots on apple trees on M.9 dwarfing rootstock had longer floral zones and higher probabilities of flower induction (within the floral zone) than trees on vigorous MM.106 rootstock (Seleznyova et al. 2004). Interstems of M.9 and M.27 have also been reported to increase cropping in apples (Di Vaio et al. 2009). Following these experimental observations, the competition theory asserts that at least some of the rootstock-induced size control of fruit trees on selected rootstocks is caused by precocious cropping that indirectly controls vegetative growth.

This theory is supported by several early studies. Jackson (2003) reported data collected by Barlow and Smith at the East Malling Research station in the early 1970s. This experiment with 13-year-old apple trees grafted on dwarfing M.9 and invigorating M.16 rootstocks compared trees that were completely deblossomed from planting and trees that were allowed to crop regularly. Over 13 years, cropping trees on M.9 accumulated around 10% of the amount of dry matter partitioned to vegetative growth of trees on M.16. In contrast, vegetative growth differences between deblossomed trees on the two rootstocks were smaller (around 20%). This difference was related to the fact that in trees on M.9, the dry matter increment partitioned to vegetative growth (cumulated over a 13-year period) induced by blossom removal was higher than in trees on M.16. Similarly, Avery (1970) compared fruited and deblossomed 'Worcester Pearmain' apple trees grafted on four rootstocks with differing vigor (3426, M.2, M.26, and 3430). Their results suggest that competition between vegetative and reproductive growth may be higher in trees grafted on size-controlling rootstocks than on invigorating rootstocks. Similar behavior may be true for peach. Basile et al. (2007) reported that fine root production of peach trees grafted on the dwarfing K146-43 rootstock was stimulated by fruit removal at harvest more than in trees on invigorating rootstocks.

Furthermore, as reported in this chapter, the growth of early shoots of bearing 'Worcester Pearmain' apple trees grafted on M.9 terminated significantly earlier than trees on M.2 (Avery 1969). However, in the same study (Avery 1969), the length of the growth period of early shoots of apple trees on M.9 was increased significantly (and similar to that of bearing and deblossomed trees on M.2) when trees were deblossomed (flower removal did not affect the length of shoot-growing period of tree on M.2).

In an architectural study, Costes and García-Villanueva (2007) compared the vegetative and reproductive growth of apple trees, either own-rooted or grafted on 'M.9' rootstock, three years after transplanting one-year-old trees into the field. The dwarfing M.9 strongly affected the flowering behavior of the trees (by increasing the occurrence of axillary flowers, the probability of terminal flowering, and the probability of return bloom). The effects of size-controlling rootstocks on vegetative growth and canopy architecture (reduced numbers of axes per tree, lower proportions of long axes, and increased proportions of medium axes and spurs in trees grafted on M.9 compared to own-rooted trees) appeared only after flowering occurred. Lauri et al. (2006) suggested that apple trees on dwarfing rootstocks are, from an architectural point of view, "physiologically older" (have shorter annual shoots, are more precocious, and have higher meristem differentiation) compared to trees on invigorating rootstocks. This hypothesis was further confirmed by the architectural study from Seleznyova et al. (2008), indicating that the early transition to flowering in apple trees on M.9 rootstocks during the first growing season after grafting shifted annual growth from mainly monopodial to sympodial branching (that characterizes apple vegetative and floral shoots, respectively). This study reported that, independent of whether M.9 was used as a rootstock or interstock, the effects on axillary annual shoots were similar. This, as well as many other interstem studies, suggests that the dwarfing mechanism of many dwarfing rootstocks is not entirely related to the root system.

Lliso et al. (2004) studied the dwarfing mechanism of 'Navelina' orange trees grafted on two dwarfing rootstocks (F&A 418 and #23) using trees on the nondwarfing #24 as a control. Most of their results appeared to be consistent with the competition theory of rootstock-induced dwarfism. They reported that: (i) yield efficiency (expressed as both number and fresh mass of fruit per unit canopy volume) increased with increasing size-controlling potential of the rootstock, (ii) defruiting trees on the size-controlling rootstocks strongly stimulated summer shoot sprouting, and (iii) sucrose concentration in fruit (expressed both as milligrams of sucrose per gram of fruit dry mass and as grams of sucrose per cubic meter of canopy) and in fibrous roots was significantly higher in trees on dwarfing rootstocks than on invigorating rootstocks (with no effect of rootstock on leaf CO_2-exchange rate). The same experiments appeared to exclude involvement of hormone action in the dwarfing mechanism of these rootstocks.

However, competition caused by precocious fruiting does not appear to explain the dwarfing response observed in some species or in some scion–rootstock combinations. The relationship between vigor-controlling potential of a rootstock and its effect on increased cropping capacity cannot be considered a rule even in apples. M.25 is an invigorating apple rootstock that induces precocious flowering and cropping. Conversely, Inmil (GM.9) and Damil (GM.61/1) sweet cherry rootstocks are dwarfing but induce relatively poor floral precocity in scions (Webster 1995). The capacity of a rootstock to induce cropping precocity and decrease vigor in the scion is very important because both features have large positive economic implications. Thus, in most breeding programs, clonal selection considers both characteristics positively, and it is possible that genotypes having both features have had high probabilities of being selected. Thus, the inevitable effect of early cropping on the whole-tree cumulative vegetative growth over the years should not be overlooked, but these two characteristics are not always linked. In addition, the competition theory does not entirely explain the effect of dwarfing rootstocks on shoot extension growth of both main and sylleptic shoots that has been reported in one-year-old vegetative apple trees grafted on M.9 compared to trees on more invigorating rootstocks (van Hooijdonk et al. 2011).

G. Other Possible Contributions to the Rootstock-Induced Dwarfing Mechanism

It is well known from common pruning practice that artificially increasing the branching angle is a powerful tool that growers have to control tree vigor and favor reproductive growth (Faust 1989). Various authors have reported that some apple (Webster 2004) and cherry (Warner 1991; Osterc and Spethmann 2002) size-controlling rootstocks induced wide branching angles in the scion. However, Webster (2004) questioned whether the influence of dwarfing rootstocks on branching angle is a direct rootstock effect or is indirectly related to early branch bending due to the increased cropping precocity induced by these rootstocks, or both. In addition, the effect of size-controlling apple rootstocks on branch angle depends on the cultivar (Tworkoski and Miller 2007). Furthermore, Weibel et al. (2003) reported that size-controlling peach rootstocks did not significantly affect branching angle. If there is a connection between branch angle and dwarfing for some rootstocks, it is likely that the response is connected to a resource competition effect because more horizontal branches have a greater tendency to produce fruit (Faust 1989).

Several viruses and viroids have also been reported to induce dwarfism in plants (Fraser and Whenham 1982; Flores et al. 2005). The citrus exocortis viroid induces dwarfism in citrus trees apparently by increasing the hydraulic resistance of the above-ground system (Moreshet et al. 1998). Interestingly, when dwarfing M.9 apple rootstock was heat-treated to produce the virus-free M.9 EMLA rootstock, it was reported to have lost some of its size-controlling potential (Ferree and Carlson 1987). Campbell (1981) demonstrated that part of the lost size-controlling potential of M.9 EMLA could be restored by inoculating the rootstocks with latent virus. Thus, it appears that latent viruses may also explain part of the size-controlling capacity of some rootstocks.

IV. CONCLUSIONS

Several theories have been proposed for the dwarfing mechanism involved in controlling scion vigor or growth by specific rootstocks in several different fruit tree species. Most of these theories are backed by experimental data in various species, but none of the theories have been documented to be the only mechanism involved to the exclusion of all others. Although graft compatibility is a requirement for any commercially viable scion–rootstock combination, this does not mean that some partial incompatibility that alters transport of water, nutrients, carbohydrates, or hormones across the graft union could not be involved in the size-controlling phenomenon. This seems particularly likely when there are external signs of partial incompatibility like severe scion overgrowth or undergrowth relative to the rootstock, or when grafted trees produce copious root suckers compared to the same rootstock genotype grown without a scion.

While hormone-based theories have traditionally been the most prevalent among horticulturists because of early studies of hormone concentrations, it is difficult to assign causality due to hormonal regulation of growth of the scion by rootstocks based on differences in concentrations or transport of hormones in the scion. If there is a water relations or nutrient-based limitation in growth of the scion caused by reduced uptake of the rootstock, it is likely that shoots exhibiting less vigorous growth would intrinsically have lower concentrations of growth-stimulating hormones. Dynamic simulation models of plant and crop growth are routinely constructed without considering hormonal control of plant development and growth because plant development and growth are primarily driven by exogenous variables like radiation, temperature, and access to resources such as water and nutrients (de Wit and Penning de Vries 1983). Indeed, the growth and development of a peach tree on a dwarfing rootstock in comparison with a tree on a vigorous rootstock have been successfully simulated with the L-Peach model without directly considering interactions among plant hormones (Da Silva et al. 2015). This is possible because the hormonal system in plants is primarily a communication system for conveying messages within and among organs (de Wit and Penning de Vries 1983), but hormones themselves are not the source of the messages. It is highly likely that the messages that are conveyed among and within some organs (especially shoots) growing on scions on dwarfing rootstocks are altered compared to the same scions on vigorous rootstocks, but that does not mean that they are the cause of the dwarfing. The challenge for researchers involved in conducting dwarfing rootstock research from the hormonal perspective is to determine whether the altered growth behavior of scions on dwarfing rootstocks is a function of different messages being sent or because of messages being altered during the process of transporting the message in trees on dwarfing rootstocks. If it is the former, then the goal is to find the nonhormonal source of the different messages. If it is the latter, one has to determine how the messages are systematically changed so that growth characteristics are consistent and specific to each rootstock–scion combination.

Of all the mechanisms discussed in this review that would evoke changes in the sources of hormonal messages transported within trees, the water uptake and transport mechanism appears to be the most strongly supported. Both functional (differences in stem water potential and hydraulic conductance) and anatomical (xylem characteristics) evidence for it has been reported in several species. However, this evidence has generally not been provided to the exclusion of most of the other mechanisms. The study of dwarfing mechanisms is very complex, and the multiple factors that may be involved often complicate the interpretation of the results. Even if the water relations mechanism is the primary causal mechanism in specific cases, once it is in play, it is likely to affect the balance of several other factors such as carbohydrate and nutrient supplies and distribution.

Many studies have focused on young trees. Extrapolations of these results to mature trees should be viewed with caution. Most of the effects of dwarfing rootstocks on vegetative growth are cumulative with time, and multiple factors are simultaneously at play as a fruit tree grows. For instance, if a tree is initially less vigorous because of its rootstock, it will likely receive less pruning, and its branches will likely be less shaded. Less pruning will result in less pruning-induced stimulation of shoot growth, and less shading will likely lead to greater flower production. Both of these factors tend toward decreased tree vigor in subsequent growth cycles. Therefore, the interpretation of the results of studies on mature trees can be complex and sometimes misleading if they only consider a single year of study.

Another limitation of most research on the functional mechanisms involved in rootstock-induced dwarfing of fruit trees is the lack of comprehensive studies that consider multiple potential mechanisms to develop unified theories without starting from some bias favoring one individual theory over others. A comprehensive general understanding of root–shoot interactions and the factors that control tree growth and development is necessary before it is possible to sort out the primary mechanisms involved in the rootstock-induced scion dwarfing characteristics of specific scion–rootstock combinations. It is clear that in the case of many of the commonly used dwarfing rootstocks, comprehensive theories concerning size-controlling mechanisms also need to explain tree growth behaviors when the rootstock genotype is used as interstocks. Given the research that has been done, it appears likely that aspects of the mechanisms involved vary among fruit tree species and the scion and rootstock genotypes used. Thus, it will likely be necessary to develop species- or genotype-specific theories to explain growth responses of many of the rootstock–scion combinations.

Virtually all dwarfing fruit tree rootstocks currently used commercially have been derived from empirical studies with little initial understanding of the mechanisms causing the dwarfing. As more knowledge about these mechanisms becomes available, it should be possible to develop genetic markers for identifying genotypes that have the functional traits related to specific mechanisms. Such advances will enable more definitive studies of the mechanisms involved in existing dwarfing rootstock–scion combinations and greatly improve the efficiency of developing new and improved rootstocks for fruit tree cultivation.

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