

Defense Mechanisms Involved in Disease Resistance of Grafted Vegetables

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Abstract. Grafting with resistant rootstocks is an effective strategy to manage a variety of soilborne diseases and root-knot nematodes in solanaceous and cucurbitaceous vegetables. In addition, improved resistance to some foliar diseases and viruses has also been reported in grafted plants. Hence, grafting technology is considered an important and innovative practice of integrated pest management and a promising alternative for soil fumigants in vegetable production. Inherent resistance within rootstocks and improved plant nutrient uptake are generally suggested as the main reasons for improved disease control in grafted vegetables. However, increasing evidence indicated that systemic defense mechanisms may also play an important role in plant defense as a result of grafting. This review analyzes current literature on the use of grafting techniques for disease management in vegetable crops, discusses potential mechanisms associated with grafting-conferred plant defense, and identifies needs for future research to promote more effective and efficient use of grafting technology to support sustainable vegetable production.

Grafting, with selected resistant rootstocks, for the purpose of controlling diseases and pests is an ancient practice widely used in cultivating a variety of woody trees. Some of the well-known examples include controlling tristeza on citrus, fireblight and collar rot on apples, and nematodes on peaches and walnuts (Mudge et al., 2009).

Research on herbaceous vegetable grafting began in the 1920s with watermelon [*Citrullus lanatus* (Thunb.) Matsum. & Nakai] grafted onto squash rootstocks (*Cucurbita moschata* Duch.) to overcome yield loss caused by fusarium wilt (Sato and Takamatsu, 1930). Since then, grafting has been widely used in Asia and European countries as an effective tool for managing several soilborne diseases and root-knot nematodes in the Solanaceae and Cucurbitaceae. Interest in vegetable grafting has recently grown in the United States as an alternative to soil fumigants and as an integrated pest management practice in various crop production systems (Kubota et al., 2008).

A few reviews have been published recently, which address the integrated use of grafting techniques in vegetable production. Among them, a review by Lee and Oda (2003) covered topics including grafting methods and procedures, grafting physiology, and production status of grafted vegetables and ornamental crops. Cucurbit grafting including the history, current status, and benefits of vegetable grafting were well documented by Davis and colleagues (2008). Louws and coauthors (2010) summarized current literature on use of grafting technology to manage diseases and pests in vegetable production. The review provided up-to-date information on disease cycles, current disease management practices, and effects of rootstocks on controlling different pathotypes. Some important disease resistance mechanisms were mentioned, whereas systematic discussion of this topic was rather limited.

Unlike previous work, the current review explores specifically the defense mechanisms in grafted vegetable plants and discusses future research initiatives needed to advance our understanding of the underlying grafting mechanisms and to enhance vegetable rootstock breeding programs.

Diseases Controlled by Grafting in Vegetable Production

Improved resistances to many soilborne fungal, oomycete, bacterial, and nematode

pathogens have been reported in grafted solanaceous and cucurbitaceous crops. Moreover, certain foliar fungal and viral diseases were suppressed when susceptible scions were grafted onto specific rootstocks (Louws et al., 2010). Diseases controlled by grafting in different vegetable crops are listed in Table 1.

Soilborne fungal and oomycete diseases.

The earliest reported use of vegetable grafting for disease control was for management of fusarium wilt in cucurbits (Sakata et al., 2005). Commonly used cucurbitaceous rootstocks are non-hosts to most formae speciales of *F. oxysporum*, and thus grafting has been successfully used to control fusarium wilt in cucurbit production (Louws et al., 2010). Verticillium wilt, primarily caused by *Verticillium dahliae*, is another vascular wilt disease that often affects Solanaceae and Cucurbitaceae. Studies with plants grafted onto commercial rootstocks and subjected to infection with *V. dahliae* indicated that both scions and rootstocks contributed to disease resistance of the grafted combinations in watermelons, melons (*Cucumis melo* L.), cucumbers (*Cucumis sativus* L.), and tomatoes (*Solanum lycopersicum* L.) (Paplomatas et al., 2002). *Monosporascus sudden wilt*, caused by *Monosporascus cannonballus*, is an important soilborne disease of melon and watermelon in hot and semiarid areas. Grafting scions of susceptible melon cultivars onto *C. maxima* Duch. and *C. maxima* × *C. moschata* rootstocks improved resistance of melon (Edelstein et al., 1999) although *Cucurbita* is normally regarded as a host for *M. cannonballus* (Mertely et al., 1993). However, the improved resistance and better yield with grafted plants was inconsistent. The variable results might be attributed to differences in rootstock–scion combinations and growing conditions. Phytophthora blight, caused by *Phytophthora capsici*, is regarded as one of the most destructive diseases in production of cucurbits. In *P. capsici*-infested fields, yields of cucumbers grafted on bottle gourd [*Lagenaria siceraria* (Mol.) Standl.], *C. moschata* Duch., and wax gourd [*Benincasa hispida* (Thunb.) Cogn.] rootstocks were significantly increased and vegetative growth was more vigorous (Wang et al., 2004). Watermelons grafted onto selected bottle gourd rootstocks also exhibited resistance to *P. capsici* (Kousik and Thies, 2010). Corky root disease caused by *Pyrenochaeta lycopersici* is a severe problem for Solanaceae. Tomatoes grafted onto ‘Beaufort’ rootstocks (*S. lycopersicum* × *S. habrochaites* S. Knapp & D.M. Spooner) had lower disease incidence, higher yield, and larger fruit (Hasna et al., 2009). Similar results were also found in grafted eggplants (*S. melongena* L.) (Iouannou, 2001).

Soilborne bacterial diseases. Tomato bacterial wilt, caused by *Ralstonia solanacearum*, is one of the most destructive diseases of tomato. Resistance to bacterial wilt in tomatoes is a quantitative trait and is closely associated with small fruit size (Louws et al., 2010). Thus, few resistant tomato cultivars are commercially available (King et al., 2010). Grafting scions of susceptible tomato cultivars onto

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Table 1. Diseases reported to be controlled by grafting in different vegetable crops.

Disease and pest	Pathogen	Crops
Fungal and oomycete diseases		
Fusarium wilt	<i>Fusarium oxysporum</i>	Tomato, pepper, watermelon, melon, cucumber
Fusarium crown and root rot	<i>Fusarium oxysporum</i> ; <i>Fusarium solani</i>	Tomato, pepper, watermelon
Verticillium wilt	<i>Verticillium dahliae</i>	Tomato, eggplant, watermelon, melon, cucumber
Monosporascus sudden wilt	<i>Monosporascus cannonballus</i>	Watermelon, melon
Phytophthora blight	<i>Phytophthora capsici</i>	Tomato, pepper, watermelon, cucumber
Corky root	<i>Pyrenochaeta lycopersici</i>	Tomato, eggplant
Target leaf spot	<i>Corynespora cassiicola</i>	Cucumber
Black root rot	<i>Phomopsis sclerotoides</i>	Cucumber, melon
Gummy stem blight	<i>Didymella bryoniae</i>	Melon
Southern blight	<i>Sclerotium rolfsii</i>	Tomato
Brown root rot	<i>Colletotrichum coccodes</i>	Tomato, eggplant
Rhizoctonia damping off	<i>Rhizoctonia solani</i>	Tomato
Powdery mildew	<i>Podosphaera xanthii</i>	Cucumber
Downy mildew	<i>Pseudoperonospora cubensis</i>	Cucumber
Bacterial diseases		
Bacterial wilt	<i>Ralstonia solanacearum</i>	Tomato, pepper, eggplant
Nematodes		
Root-knot	<i>Meloidogyne</i> spp.	Cucumber, melon, watermelon, tomato, eggplant, pepper
Viral diseases		
Melon necrotic spot virus	<i>Melon necrotic spot virus</i> (MNSV)	Watermelon
Tomato yellow leaf curl	<i>Tomato yellow leaf curl virus</i> (TYLCV)	Tomato
Tomato spotted wilt	<i>Tomato spotted wilt virus</i> (TSWV)	Tomato
Pepino mosaic virus	<i>Pepino mosaic virus</i> (PepMV)	Tomato

Information was adapted from published reviews (King et al., 2008; Louws et al., 2010).

resistant rootstocks has been successful for managing tomato bacterial wilt (Lin et al., 2008; Matsuzoe et al., 1993). The improved resistance in grafted plants may result from limited colonization in the lower stem rather than prevention of bacteria from invading xylem tissues (Grimault and Prior, 1994).

Root-knot nematodes. Root galling of susceptible plants is a typical response to root-knot nematode (RKN; *Meloidogyne* spp.) infection, resulting in poor absorption of water and nutrients. In cucurbits, resistance to *M. incognita* was identified in *Cucumis metuliferus* Naud., *Cucumis ficifolius* A. Rich., and bur cucumber (*Sicyos angulatus* L.) (Fassuliotis, 1970; Gu et al., 2006). Using *C. metuliferus* as a rootstock to graft RKN-susceptible melons led to lower levels of root galling and nematode numbers at harvest (Sigüenza et al., 2005). Moreover, *C. metuliferus* showed high graft compatibility with several melon cultivars (Trionfetti Nisini et al., 2002). Cucumbers grafted on the bur cucumber rootstock exhibited increased RKN resistance (Zhang et al., 2006). Promising progress has also been made in developing *M. incognita*-resistant germplasm lines of wild watermelon [*Citrullus lanatus* (Thunb.) Matsum. & Nakai var. *citroides* (L. H. Bailey) Mansf.] for use as rootstocks (Thies et al., 2010). However, at present, cucurbit rootstocks with resistance to RKN are not commercially available (Thies et al., 2010). The *Mi* gene, which provides effective control against RKN in tomato, has been introgressed into cultivated tomatoes and rootstock cultivars (Louws et al., 2010). Grafting of susceptible tomato cultivars on RKN-resistant rootstocks was effective in controlling RKN in fields

naturally infested with RKN (Rivard et al., 2010). However, as a result of temperature sensitivity of the *Mi* gene, such resistance may not be uniformly stable (Cortada et al., 2009). Pepper (*Capsicum annuum* L.) cultivars possessing the *N* gene, which controls resistance to RKNs (*M. incognita*, *M. arenaria*, and *M. javanica*), have been effective as rootstocks to control RKNs in pepper (Oka et al., 2004; Thies and Fery, 1998, 2000).

Viral diseases. Vegetable grafting research on resistance to viral diseases yielded mixed results because of the lack of systematic studies in this area. Wang et al. (2002) reported improved antiviral performance in grafted seedless watermelon plants. In Israel, use of resistant rootstocks for controlling the soilborne *melon necrotic spot virus* in cucurbits was a significant advantage over soil fumigation with methyl bromide, which does not control this viral disease (Cohen et al., 2007). Meanwhile, *tomato yellow leaf curl virus*, *tomato spotted wilt virus*, and *pepino mosaic virus* were also reported to be controlled by grafting (Louws et al., 2010). However, some reports indicated that grafted plants were more vulnerable to viral diseases, possibly as a result of graft incompatibility that weakened the scion plants (Davis et al., 2008).

Other diseases. Other fungal diseases that have been controlled by grafting include target leaf spot (caused by *Corynespora cassiicola*) on cucumbers, black root rot (caused by *Phomopsis sclerotoides*) on cucumbers and melons, gummy stem blight (caused by *Didymella bryoniae*) on melons, southern blight (caused by *Sclerotium rolfsii*) on tomatoes, brown root rot (caused by

Colletotrichum coccodes) on tomatoes and eggplants, and Rhizoctonia damping off (caused by *Rhizoctonia solani*) on tomatoes (King et al., 2008; Louws et al., 2010) (Table 1). Grafting has also been reported to improve crop resistance to the foliar fungal diseases such as powdery mildew (caused by *Podosphaera xanthii*) and downy mildew (caused by *Pseudoperonospora cubensis*) on cucumbers, when certain rootstocks were used (Louws et al., 2010; Sakata et al., 2006).

Inherent Resistance within Rootstocks as the First Line of Defense

Because grafting is used primarily for controlling soilborne diseases, the defense mechanisms are generally associated with inherent resistance within rootstocks (King et al., 2008). Rootstock selection and breeding has targeted both non-host and host resistance.

Using non-host resistance. Non-host disease resistance refers to the resistance provided by all members of a plant species against all races of a certain pathogen and it is often considered the most common and durable plant disease resistance (Mysore and Ryu, 2004). Solanaceous vegetables and cucurbits are often grafted onto rootstocks that, although related, are different species or hybrids of different species. Taking advantage of the non-host resistance in these rootstocks is a convenient approach to battling specific pathogens that infect the cultivated scion species but not the rootstock species. For example, *F. oxysporum* f. sp. *niveum* causes disease specifically on watermelon and *F. oxysporum* f. sp. *lagenaria* typically infects bottle gourd (Namiki et al., 1994). Because all of the bottle gourd genotypes offer resistance to all races of *F. oxysporum* f. sp. *niveum* (race 0, 1, 2), non-host resistance has been proven to be a viable mechanism to control fusarium wilt in watermelons when they are grafted onto bottle gourd rootstocks (Yetisir et al., 2007).

Breeding host-resistant rootstocks. Although interspecific grafting, i.e., grafting between scion and rootstock that are not from the same species, is often conducted to use the non-host resistance in the rootstock, intraspecific grafting, i.e., grafting between scion and rootstock that are from the same species, is also commonly performed, especially when host-resistant rootstocks are available. Sometimes intraspecific grafting may be preferred because it helps enhance graft compatibility and reduce potential detrimental effects on fruit quality in comparison with interspecific grafting.

Host resistance can be generally classified into two categories: vertical resistance and horizontal resistance. Vertical resistance is governed by single genes that lead to large and differential effects, whereas horizontal resistance is controlled by multiple genes with small and nondifferential effects (Fry, 1982). Oftentimes, the horizontal resistance can be unintentionally lost by continuous selection for horticultural characteristics. Many cucurbitaceous and solanaceous rootstocks are

selected from wild germplasm, and thus they are more likely to maintain nondifferential resistance to a wide range of pathogens. During the past decades, considerable efforts have been directed into breeding plants with resistance (*R*) genes against distinct pathogens. However, combining a complete set of desirable traits including horticultural characteristics and resistance to multiple diseases into a single variety is rather challenging and sometimes can be contradictory. The close linkage between resistance against bacterial wilt in the Solanaceae and small fruit size is such an example (Louws et al., 2010). Through the use of grafting, the breeding programs can become more efficient and effective by focusing on above- and below-ground traits separately and combining disease resistance and other horticultural traits into a so-called “graft hybrid” (Mudge et al., 2009).

Vertical resistance is often governed by cascade reactions initiated by interactions of *R* genes of plants with avirulence (*avr*) genes of pathogens, which is known as a gene-for-gene hypothesis (Flor, 1971). Identification of *R* genes as well as its downstream signal transduction is always the key to understanding host resistance. *R* genes have been identified in many cucurbitaceous and solanaceous rootstocks. One of the examples is the *Mi* gene, which confers resistance to *M. incognita*, *M. javanica*, and *M. arenaria* in tomato. This resistance involves hypersensitive responses and reactive oxygen production at the feeding site, restricting the establishment of the RKN juveniles (Fuller et al., 2008). In the case of combating fusarium wilt of melons caused by four races (0, 1, 2, and 1.2) of *F. oxysporum* f. sp. *melonis* (FOM), commercial melon cultivars containing two *R* genes (*Fom-1* and *Fom-2*) provide resistance to FOM 0, 1, and 2 but fail to control FOM 1.2. With resistance to FOM 1.2 identified in new breeding lines and indigenous cultivars of *C. melo* (Herman and Perl-Treves, 2007; Hirai et al., 2002), grafting susceptible cultivars onto resistant rootstocks can be an effective and efficient method to control FOM 1.2 given that FOM 1.2 resistance is polygenically inherited.

Proteins encoded by *R* genes may play a direct role in detoxification of toxins or activation of plant defense by initiating signal transduction. Interestingly, several common features have been identified among *R* gene-encoded proteins from different species such as the leucine zipper region, nucleotide binding site, and leucine-rich repeats, suggesting a common pathway of plant defense against a variety of pathogens (Hammond-Kosack and Jones, 1997).

Developing transgenic rootstocks. In addition to use of non-host-resistant rootstocks as well as selection and breeding for host resistance from a wide range of germplasm, transgenic rootstocks with specific disease resistances have been developed. For example, a *cucumber green mottle mosaic virus* coat protein gene and a *cucumber fruit mottle mosaic tobamovirus* replicase gene were introduced into watermelon and cucumber rootstocks,

respectively. Susceptible scions grafted onto transgenic rootstocks exhibited high resistance against viral pathogens (Gal-On et al., 2005; Park et al., 2005; Yi et al., 2009).

Future prospects. Using rootstocks with non-host resistance has been shown as an effective tactic in controlling fusarium wilt in cucurbits. However, this method may increase risk of graft incompatibility if rootstocks and scions are not from the same species or genus. For example, figleaf gourd (*Cucurbita ficifolia* Bouché) is incompatible with oriental melons and watermelons, whereas wax gourd is incompatible with oriental melons (Lee and Oda, 2003). Considering the variation of graft compatibility between even closely related species, it is always suggested to test graft compatibility before considering the use of non-host-resistant rootstocks for soilborne disease control.

Regardless of the advancement in rootstock resistance research, many fundamental areas are still poorly understood, including the effects of grafting and scion feedback on the inherent resistance of rootstocks. Jiang et al. (2010a) observed that grafted peppers had a lower incidence of fusarium root rot than self-rooted scion plants, whereas non-grafted rootstock plants showed the lowest disease incidence. It indicated that scion feedback may potentially influence rootstock resistance. As a result of the lack of in-depth studies on rootstock defense mechanisms, it is even more challenging to determine the effect of various scion cultivars on rootstock resistance. Elucidating the interactions of scions and rootstocks would greatly enhance our understanding of disease resistance of grafted vegetables.

Shift of Rhizosphere Microbial Diversity as a Result of Grafting

Rhizosphere microorganisms can play critical roles in suppressing soilborne diseases through a variety of mechanisms such as nutrient competition, antagonism, and parasitism. Exploring rhizosphere microbial diversity related to plant species and genotypes, therefore, is another approach to understanding soilborne disease incidence and severity (Broeckling et al., 2008; Garbeva et al., 2004; Yao and Wu, 2010).

Studies on cucumbers grafted onto *C. moschata* indicated that grafting increased the population of bacteria and actinomycetes while reducing the total number of fungi in the rhizosphere (Dong et al., 2010). Research on grafted peppers also showed that actinomycete populations in the rhizosphere were higher in the resistant rootstock and grafted plants compared with the self-rooted scion control when plants were inoculated with *F. solani* (Jiang et al., 2010a). Incidence of verticillium wilt was reduced when a susceptible eggplant scion was grafted onto *Solanum torvum* rootstock accompanied by enhanced ratios of bacteria and actinomycetes to fungi in the rhizosphere of grafted plants (Yin et al., 2008). Actinomycetes represent

a group of soil microorganisms with great potential to protect plants against pathogens (Doubou et al., 2001). Although it is still uncertain about the extent to which actinomycetes contribute to plant disease control, higher populations of actinomycetes detected in the rhizosphere of grafted plants could possibly play a role in disease suppression when susceptible scions are grafted onto certain resistant rootstocks.

Future prospects. Microbial communities in the rhizosphere are highly diversified and influenced by several factors including plant species, soil types, management practices, and environmental conditions (Garbeva et al., 2004). Although microbial shifts in rhizospheres of grafted plants have been observed in some studies and remain an intriguing area for study, little is known about how these shifts are related to the intrinsic resistance of the rootstock and what processes directly cause such shifts. Some of the grafting research has focused on comparison of grafted plants to self-rooted scion plants without including non-grafted rootstock plants as a positive control. To better understand effects of grafting on rhizosphere microbial diversity, non-grafted rootstock plants as well as non-grafted and self-grafted scion control plants should all be evaluated. Furthermore, long-term grafting studies with different resistant rootstocks, soil types, and management practices are warranted to clearly elucidate the influence of grafting on soil microbial diversity as related to soilborne disease control.

Contributions of Vigorous Root Systems of Grafted Vegetables to Plant Defense

Many rootstocks developed for vegetable grafting were selected or bred from wild genotypes. In addition to specific disease resistance, they are characterized by large and vigorous root systems (Davis et al., 2008; Lee, 1994). Soilborne pathogens often infect and damage plant roots, and, as a result, plant nutrient and water uptake can be affected. Therefore, root system size and vigor may be associated with resistance to soilborne diseases. Moreover, vigorous roots help improve nutritional status and thus the overall health of plants, which may augment resistance against foliar diseases.

Improved nutrient uptake in grafted vegetables. Efficiency of nitrogen uptake and use can be improved by grafting vegetables onto vigorous rootstocks (Colla et al., 2010a). Melon grafted onto *C. maxima* × *C. moschata* rootstocks exhibited higher nitrate concentration in xylem sap than that of self-rooted melon plants (Salehi et al., 2010). In addition, foliar nitrate concentrations were lower in grafted watermelons and melons accompanied by higher nitrate reductase activities in comparison with self-rooted plants, which suggests an elevated level of nitrogen assimilation in grafted plants (Pulgar et al., 2000; Ruiz and Romero, 1999). Phosphorus is a macronutrient that often limits plant growth as a result of its low mobility in the soil. Phosphorus uptake can be enhanced by

grafting with vigorous rootstocks as confirmed by analyzing phosphorus concentrations in plant tissues of grafted eggplants (Leonardi and Giuffrida, 2006), melons (Salehi et al., 2010), and watermelons (Colla et al., 2010b). However, variable results were obtained when different rootstocks and rootstock/scion combinations were used. In addition, enhanced absorption of potassium, calcium, and magnesium was also observed in grafted vegetables (Fernández-García et al., 2004; Leonardi and Giuffrida, 2006). A recent review by Savvas et al. (2010) summarized the research findings on mineral nutrient uptake in fruit vegetables as a result of grafting with specific rootstocks.

Nutrient uptake in relation to disease development. Plant nutrients, in addition to their essential roles in plant growth and development, can be directly involved in plant defense pathways. For example, foliar application of phosphate salts can induce systemic protection against anthracnose in cucumbers (Gottstein and Kuć, 1989), and phosphate-mediated resistance induction has been associated with localized cell death (Walters and Murray, 1992). Nitrogen deficiency can compromise elicitor-induced resistance to pathogen infection (Dietrich et al., 2004), whereas excessive nitrogen increases disease incidence by promoting growth of large plant canopies (Simón et al., 2003). In addition, many other mineral nutrients such as potassium, calcium, sulfur, and micronutrients also play significant roles in plant defense mechanisms (Walters and Bingham, 2007).

Future prospects. Although improved nutrient uptake of grafted vegetable plants might be related to grafting-conferred disease control, direct evidence is missing at present. Most currently reported grafting experiments on nutrient uptake were conducted under growing conditions without disease pressure. It would be interesting to use disease-resistant and vigorous rootstocks to study absorption and functions of critical nutrients in the context of plant defense against specific pathogens. Previous research has dem-

onstrated the influence of mineral nutrients on plant disease development. Several mineral elements, including silicon, have been suggested to play critical roles in plant defense (Savant et al., 1996). Hasama et al. (1993) showed that the increase of susceptibility to target leaf spot in grafted cucumbers with a tested rootstock might be related to reduced uptake of silicon because grafted cucumber plants with the other rootstock demonstrated improved disease resistance and a higher level of silicon absorption. Whether vigorous rootstocks could potentially improve the uptake of silicon and other mineral elements is unknown. Exploring these questions in future research would be an intriguing topic not only for vegetable grafting, but also for plant pathology and nutrition studies.

Grafting-induced Systemic Defense

Plant defense to pathogen attack takes place primarily at two levels. The first level involves the production of physical barriers, e.g., trichomes, to prevent or restrict pathogen invasions. The second level is derived from systemic plant defense mechanisms. A diverse range of defense responses are activated by plant-pathogen recognition. Among these responses are accumulation of reactive oxygen species (ROS), production of antimicrobial compounds, expression of pathogenesis-related genes, synthesis of nitric oxide, and hypersensitive responses (Buchanan et al. 2000). Defense responses are vital for plants; however, these responses are also metabolically expensive. Several pre-conditioning stimuli have been investigated, including pathogen attack, in which infection by a specific type of pathogen may induce long-lasting and broad-spectrum disease resistance to subsequent infections; such resistance is known as systemic acquired resistance (Durrant and Dong, 2004). In addition, pre-conditioning can include plant growth-promoting rhizobacteria, which can reduce diseases in above-ground plant parts through the induction of systemic resistance (van Loon, 2007).

Moreover, systemic defense responses may be triggered by localized tissue damage in plants (Schillmiller and Howe, 2005).

Does grafting with rootstocks induce systemic defense? A proteomics study of leaves from cucumber plants grafted onto *C. moschata* and leaves from self-rooted cucumbers showed that the expression of two types of proteins was significantly higher in grafted plants compared with self-rooted plants. The first protein type was related to plant defense responses, and the second type included photosynthesis-related proteins (Li et al., 2009). Gene expressions of ‘Gala’ apple trees (*Malus pumila* Mill.) grafted onto two rootstocks, one with moderate resistance to fireblight (caused by *Erwinia amylovora*) and the other susceptible to fireblight, were examined using cDNA amplified fragment length polymorphism. Interestingly, scions grafted onto the resistant rootstock showed increased expression of stress-related genes, whereas scions grafted onto the susceptible rootstock did not (Jensen et al., 2003). A similar study of eggplants grafted onto tomato rootstocks indicated altered expression of diverse functional genes. Functions of these genes ranged from metabolism, signal transduction, and stress response to cell cycle and transcription/translation (Zhang et al., 2008).

Defense-related enzymes are often induced by a variety of abiotic and biotic stresses. Studies have shown that plants grafted on certain rootstocks generally exhibit a higher activity of defense-related enzymes compared with self-rooted plants under certain stressful conditions (Table 2).

Phenylpropanoids are compounds induced by various biotic and abiotic stresses. In response to pathogen infection, phenylpropanoids can increase markedly to levels that are toxic to pathogens (Dixon and Paiva, 1995). Phenylalanine ammonia-lyase (PAL) plays a key role in the synthesis of phenylpropanoids and this enzyme activity often is considered an indicator of plant defense against pathogen attack. In response to *V. dahliae* infection, shoots and roots of grafted

Table 2. Enzymes reported with higher activities in grafted vegetables compared with self-rooted plants.

Enzymes	Scion	Rootstock	Plant tissue	Stress condition	Reference
Phenylalanine ammonia-lyase (PAL)	Eggplant	<i>Solanum torvum</i>	Roots and leaves	Inoculation of <i>V. dahliae</i>	Zhou et al., 1998
	Pepper	Pepper	Roots and leaves	Inoculation of <i>F. solani</i>	Jiang et al., 2010b
	Eggplant	<i>Solanum torvum</i>	Leaves	NaCl	Zhou et al., 2010
Antioxidant enzymes Peroxidase (POD), Superoxide dismutase (SOD), Catalase (CAT)	Eggplant	<i>Solanum torvum</i>	Leaves	NaCl	Li et al., 2006
	Cucumber	<i>Cucurbita ficifolia</i>	Leaves	NaCl	Gao et al., 2008
	Eggplant	<i>Solanum torvum</i>	Leaves	Excess of Ca(NO ₃) ₂	Wei et al., 2009
	Watermelon	<i>Lagenaria siceraria</i>	Leaves	NaCl	Zhu et al., 2008
	Tomato	Tomato	Leaves	NaCl	He et al., 2009
	Cucumber	<i>Cucurbita ficifolia</i>	Leaves	Low temperature	Gao et al., 2009a, 2009b
Polyamine synthesis-related enzymes Arginine decarboxylase (ADC), ornithine decarboxylase (ODC), S-adenosylmethionine decarboxylase (SAMDC)	Cucumber	<i>Cucurbita ficifolia</i>	Roots	Copper	Zhang et al., 2010

eggplant had higher PAL activity than self-rooted plants (Zhou et al., 1998). Similarly, PAL activity in roots of grafted pepper was higher in comparison with the self-rooted control both before and after inoculation with *F. solani*. Phenolic and lignin contents in leaves and roots of grafted plants were also higher than that of self-rooted plants after inoculation with *F. solani* (Jiang et al., 2010b).

During host–pathogen interactions, ROS can accumulate quickly and may function as antimicrobial agents that are directly toxic to pathogens or are involved in signaling to initiate plant defense cascades (Lamb and Dixon, 1997). A variety of antioxidant enzymes are associated with ROS production after pathogen attacks. Among them, peroxidase, superoxide dismutase, and catalase are directly involved in ROS detoxification. Grafted plants had higher antioxidant enzyme activities than self-rooted plants when subjected to abiotic stresses such as salinity and low temperature (Gao et al., 2008, 2009a, 2009b; He et al., 2009; Wei et al., 2009) (Table 2).

Potential signals associated with grafting-induced systemic defense. Long-distance signaling is a central aspect of induced systemic resistance. Because grafting allows physical union of root and shoot systems from different genetic backgrounds, long-distance signals may be involved in activating systemic defense in grafted plants.

In grafted cucumber studies, analysis of phloem exudates collected from both the cucumber scions and squash rootstocks provided direct evidence that some of the phloem proteins can move across graft unions (Golecki et al., 1998; Tiedemann and Carstens-Behrens, 1994). Large-scale mass spectrometry has been used to identify individual proteins with diverse functions, including structural proteins, antioxidant defense compounds, proteinase inhibitors, and RNA-binding proteins (Walz et al., 2004). It is likely that some of these mobile proteins might participate in signaling cascades associated with grafting-induced systemic defense.

Long-distance signals also may involve mRNAs and small RNAs (Kehr and Buhrtz, 2008). RNA transcripts, which have been identified in the phloem, include transcriptional regulators, genes controlling cell fate and cell cycle, phytohormone responsive genes, and metabolic genes (Lough and Lucas, 2006; Omid et al., 2007). Small interfering RNAs (siRNAs) mediate post-transcriptional gene silencing, a gene expression regulation mechanism involved in different layers of plant innate immunity (Padmanabhan et al., 2009). Given that siRNAs are transmissible across grafting unions, this would be an intriguing field in which to explore specific roles of siRNAs in grafting-induced systemic defense.

Defense-related phytohormones, particularly salicylic acid (SA) and jasmonic acid (JA), have been widely studied with respect to their involvement in plant defense responses. SA is commonly associated with

systemic acquired resistance and activates plant defense mechanisms against biotrophic and hemibiotrophic pathogens, whereas JA is usually involved in defense pathways against necrotrophic pathogens and herbivorous insects (Bari and Jones, 2009). Although grafting could possibly induce systemic defense, few studies have explored the link between grafting and defense-related phytohormones. Rivard and Louws (2007) showed that the expression of *PinIII*, a JA pathway-mediated proteinase inhibitor, was induced in tomato plants grafted on certain rootstocks.

Cytokinins are a group of plant hormones produced in the roots. It has been reported that more cytokinins could be released into xylem sap of cucumber scions grafted on figleaf gourd rootstocks than in the xylem sap of self-rooted cucumber plants (Lee et al., 2010). Aloni and coworkers (2010) pointed out that the increased level of cytokinins in xylem exudates of scions grafted onto certain vigorous rootstocks was closely linked to the improved growth and fruit yield of grafted plants. However, it is not well recognized that cytokinins are also involved in the regulation of plant defense responses against some pathogens. Global gene expression analysis of *Arabidopsis* infected by *Plasmiodiophora brassicae* indicated a downregulation of genes governing cytokinin homeostasis, whereas transgenic *Arabidopsis* overexpressing cytokinin oxidase/dehydrogenase genes showed resistance to the disease (Siemens et al., 2006). The *uni-1D* mutant in *Arabidopsis* that induced the expression of pathogenesis-related genes also caused the accumulation of cytokinins in *Arabidopsis* (Igari et al., 2008). These studies provided evidence for the possible involvement of cytokinins in plant defense responses. Nevertheless, it is still unclear whether and how the cytokinin production is directly related to disease resistance of grafted plants.

Future prospects. Grafting-induced systemic defense is an exciting field for future study. To achieve a comprehensive understanding of its potential roles in grafting-conferred disease control, it will be critical to identify potential signals involved in the process. Studies on phloem long-distance macromolecular trafficking indicated that the key signals may include proteins, mRNAs, small RNAs, and plant secondary metabolites. However, the individual roles of these signals in plant defense are not well understood. Thus, new information regarding defense related long-distance signals is needed to extend our knowledge of grafting-induced systemic defense.

The distinction between the grafting process and signal transduction between rootstock and scion also should be closely examined. Grafting can result in wounding responses that trigger changes in enzyme activities and hormonal status, and such changes may attenuate with healing of the graft union. In future research, it will be important to distinguish between the effects of the grafting process and rootstock–scion interactions. Changes in both the roots and shoots of grafted plants

need to be elucidated to gain a complete understanding of rootstock–scion interactions in induced systemic defense.

Concluding Remarks

Grafting technology has evolved into a unique component in the production of several solanaceous and cucurbitaceous vegetables for pest management and for improvement of crop productivity. The ready availability of disease-resistant rootstocks and development of highly efficient grafting techniques has led to expansion in the use of grafted plants worldwide. Previous studies have provided an enhanced understanding of grafting-conferred defense mechanisms from inherent resistance within rootstocks to induced systemic resistance. However, there is still a lack of in-depth research on rootstock–scion interactions and long-distance signaling as related to improved resistance in grafted plants. In addition to resistance to soilborne diseases and nematodes, foliar and virus disease resistances of grafted plants warrant more studies. To differentiate the grafting effect per se from rootstock–scion interactions, well-designed studies should include a complete set of non-grafted and self-grafted rootstock and scion treatments in addition to the scion–rootstock grafts. Because crosstalk may exist among pathways that cope with biotic and abiotic stresses, a comprehensive understanding of the defense mechanisms in grafted plants will greatly assist with the effective development of desirable rootstocks to serve sustainable agriculture.

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