

The Timeless Contribution of Rootstocks towards Successful Horticultural Farming: From Ancient Times to the Climate Change Era

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Grafting is a horticultural practice by which living vegetative plant organs (root, stem and/or buds) of either the same genotype or, usually, different genotypes belonging to the same species, genus, subfamily and/or family, are tightly connected to each other to form a double-compound plant. In fact, it is a method of asexual (clonal-vegetative) propagation of plants. The basal part of a grafted plant is called “rootstock” (“stock” or “understock”) that usually comprises the root system and a portion of the lower above ground plant stem (trunk). The rest above-ground part of a grafted plant is termed “scion”. Following successful grafting, the resulting composite plant continues growth as one individual organism according to its life-span genetic potential (annual, biennial or perennial). Early humans observed non-anthropogenic (natural) grafting in forest natural ecosystems and tried to mimic nature and, thus, applying grafting (artificial grafting) not only in domesticated forest ecosystems, but also to cultivated plants including fruit trees, grape vines, floricultural crops and vegetables. In the writings of the Greek physician, Hippocrates of Kos (460-377 BC), and Greek philosophers, Aristotle (384-322 BC) and Theophrastus (371-287 BC), grafting was clearly reported as a well-established agronomical practice at that time period.

From a practical perspective, the existence of words referring to the present usage of the terms “rootstock”, “stock” and/or “understock” is inextricably linked with the existence of the grafting *per se*. In fact, without artificial or natural grafting, there is no “rootstock” and *vice versa*.

Historically, critical roles of rootstocks have evolved through time periods expanding from years to millennia. This is due to dramatic changes in farming management requirements and/or environmental, climatic and phytopathological conditions existing in the field of horticultural crops -including fruits, vegetables and ornamentals- from the ancient times up to the era of climate change.

For many centuries, grafting was mainly used as a means of non-sexual (asexual) reproduction of plant genotypes which were difficult to root by using other methods of asexual propagation, such as cuttings, suckering, stooling and layering. The aim was then the

successful cultivation of genotypes with individual desirable agronomical and horticultural traits by grafting them onto pre-existed wild plants that produced commodities of inferior quality. Although the latter plants were used as rootstocks, their contribution was too specific. They were just used as a background plant, since they had simply provided their root system and a part of their vascular system to the new-composite plants formed after grafting. Through the following years and centuries, macro observations of agronomists and farmers have given motivation to intensive scientific research projects, carried out all over the world, aiming to breed and/or select new superior genotypes for using them as rootstocks.

The second half of the 19th century, the French wine industry was really in panic when the insect phylloxera (*Daktulosphaira vitifoliae* Fitch) nearly destroyed the grape and wine production. Until nowadays, this insect has never been eradicated or controlled by other chemical or cultural means and still remains a serious problem in susceptible wine/grape-producing regions globally. The ultimate solution remains the use of phylloxera resistant rootstocks, originating from native American *Vitis* species like *V. riparia*, *V. berlandieri* and *V. rupestris* (Mudge *et al.*, 2009). Additionally, from the beginning of the 20th century, the aphid-transmitted Citrus Tristeza Virus (CTV) has destroyed thousand hectares of citrus trees (more than 100 millions) all over the world, grafted on sour orange (*Citrus aurantium* L.) rootstock, which has been proved to be very susceptible to CTV. In this case, the best solution has also remained the prophylactic grafting of various citrus varieties on CTV resistant rootstocks, such as trifoliolate orange (*Poncirus trifoliata* sp.) and its grapefruit (Citrumelos) or sweet orange (Citranges) hybrids. Before the appearance of the CTV, sour orange had been widely used as a rootstock to protect citrus against harmful effects of *Phytophthora* spp (Roistacher *et al.*, 2010). Moreover, as a result of the limited availability of arable land, the high demand for off-season vegetables and the intensive production practices with limited crop rotations, vegetables are often cultivated under adverse conditions (Savvas *et al.*, 2010). In fact, the intensive continuous monoculture of vegetables has led to the establishment and exponential growth of many soil-

borne diseases, like *Verticillium* spp., *Fusarium* spp. and bacterial wilts. This resulted in serious damages in plants, lower yields and production of inferior quality commodities. To overcome this problem, in the middle of the 20th century, Japanese and Korean researchers and farmers were the first who succeeded in the large scale production of various commercial cultivars, belonging to Solanaceae and Cucurbitaceae families, grafted on appropriate disease-resistant rootstocks. Today, grafting of vegetables is a widely spread horticultural practice that is commercially exploited in many countries all over the world (Mudge *et al.*, 2009; Lee *et al.*, 2010; Schwarz *et al.*, 2010).

Although biotic factors are usually the main reasons of using rootstocks in fruit, ornamental and vegetable crops, there are many other reasons for grafting commercial varieties on different rootstocks. For example, grafting represents an important means to avoid or reduce yield losses due to salinity stress. The benefits of grafting high-productive genotypes onto salinity-resistant rootstocks include better growth and higher yield, higher photosynthesis, water content, elevated concentrations of osmoprotectants, antioxidants, abscisic acid and polyamines in leaves and lower contents of sodium and/or chloride in various plant parts, compared to un-grafted plants (Colla *et al.*, 2010; Penella *et al.*, 2016). Rootstock can also affect various aspects of plant nutrition under conditions of mineral deficiency or toxicity. Indicatively, the role of the rootstock is critical when citrus trees are cultivated in orchards irrigated with water containing high boron. More specifically, 'Clementine' mandarin and 'Navelina' orange plants grafted on 'sour orange' rootstock proved to be more sensitive to boron excess than those grafted on 'Swingle citrumelo'. This is mainly due to lower absorption of boron from the roots of 'Swingle citrumelo' and to higher boron retention in the stem of this rootstock, resulting in lesser boron accumulation in leaves of the two aforementioned cultivars when they are grafted on 'Swingle citrumelo' (Papadakis *et al.*, 2004a; 2004b).

Besides from the premium contribution of rootstocks in the adaptation of grafted varieties on adverse abiotic and biotic conditions, their effects on different stages of farm management and cultivation practices *per se* have been well documented. For instance, the use of shading nets is a common, although too expensive, procedure to decrease the impact of high solar irradiance stress during the spring-summer harvesting period, especially in Mediterranean areas. The use of some rootstocks has been reported to be an economically-efficient alternative means to maintain commercial fruit yield and quality under non-shaded greenhouse conditions (Lopez-Marin *et al.*, 2013). Therefore, the overall benefit is at least double, decreasing production costs (there is no need to buy shading nets) and protecting the environment (less

manufacture of shading nets). Similarly, rootstock can affect the overall performance of scion, when plants are exposed to suboptimal air and soil temperatures, resulting in either prompt-earlier vegetative and reproductive growth (fruit set, growth, maturation and harvest), or extension of the growing season. The respective earlier and/or delayed harvest, combining with higher yields succeeded over the time together with the production of better quality commodities, result in a significant increase of farmers' net income (Schwarz *et al.*, 2010). Finally, the establishment of high density fruit tree plantings is exclusively based on dwarfing rootstocks which not only induce scion precocity and higher yields per unit of orchard area, but also substantially decrease labor and production costs per each unit of produced fruits (Robinson, 2011).

The beneficial impacts of the rootstocks may also be extended beyond harvest. Some indicative examples are addressed below, although more research has to be carried out in the future for all related issues. Firstly, rootstock can improve the main quality indices of various harvested products, including the overall nutritive value and aromatic substances of horticultural products (Rouphael *et al.*, 2010; Orazem *et al.*, 2011; Krumbein, 2013; Legua *et al.*, 2014). They may also enhance the levels of various particular health-promoting substances (Rouphael *et al.*, 2010; Turhan *et al.*, 2011; Chavez-Mendoza *et al.*, 2013. Krumbein, 2013; Legua *et al.*, 2014; Cardenosa *et al.*, 2015) or decrease those of health hazardous ones (e.g., organic pollutants) (Schwarz *et al.*, 2010). Secondly, postharvest storage and shelf life of fruits and vegetables are also rootstock-dependent (D'Hallewin *et al.*, 1993; Ritenour *et al.*, 2004). Thirdly, the effect of rootstock may also be critical in the processing of fruits and vegetables. For instance, since pH adjustment is a significant part of the total cost of vinification, the identification of rootstocks that result in lower potassium concentrations and pH values in grape must and wine is of high interest for the wine industry (Walker and Blackmore, 2012; Bouza *et al.*, 2013), particularly in world's regions producing wine with relatively high values of pH. In the latter case, suitable rootstocks could help in reducing winemaking production cost and improving some key quality attributes of wine.

It is well-known that global warming and the impact to the environment are issues of increasing importance and a subject of international debate, mainly over the last years, attracting the attention of several scientific studies (Landi and Benelli, 2016), including research on new rootstocks. In particular, at the current era of the climate change, breeding and selecting rootstocks with specific traits (e.g., heat, drought, salinity, waterlogging and/or flooding tolerance), due to continuous changing environmental issues, will help in successful growing of fruits and vegetables even in the most affected areas worldwide. As a result of global warming, the accumulated winter chill is continuously decreasing in

many regions of the world (Baldocchi and Wong, 2008; Atkinson *et al.*, 2013), a fact that may cause serious limitations in the cultivation of temperate-zone deciduous fruit and nut tree species due to incomplete dormancy release. Based on the literature (Ghrab *et al.*, 2014), the role of rootstocks could be vital thanks to their beneficial effects on the scions' buds requirements for chilling units to overcome dormancy. However, more research is needed to evaluate more appropriate rootstock-scion combinations for areas having relatively low chilling hours. Moreover, as the climate continues to be warmer, the frequency, the intensity and the duration of serious precipitation events is expected to increase, enhancing the probability for soil waterlogging/flooding in many areas of the world (Kundzewicz *et al.*, 2014). Selecting and/or creating new rootstocks to resist anaerobic soil conditions are really important challenges for horticultural breeders.

The research on rootstocks is really multidisciplinary, requiring the contribution of different, usually well-separated, horticultural and agricultural branches. Since 1900s, huge funds have been invested worldwide in breeding, selecting and evaluating genotypes having the proper traits to be used as superior rootstocks. According to an independent assessment commissioned by the Australian Grape and Wine Authority (AGWA), every dollar invested in vine rootstock-associated research generates \$11 in return to users of rootstocks only across the Australian wine industry (AGWA, 2015).

A superior rootstock enables the genetically composite plant, *viz.* each one specific rootstock-scion combination, to adapt to a number of different factors including root- and/or shoot-associated both abiotic [e.g., drought, waterlogging, flooding, salinity, mineral toxicity, mineral deficiency, heavy metal toxicity, heat, cold, low chilling units, low soil temperature, low soil oxygen, wet or poorly drained soils, soils with high calcium carbonate content, high or low soil pH (Papadakis *et al.*, 2004a; 2004b; Colla *et al.*, 2010; Hartmann *et al.*, 2013; Savvas *et al.*, 2010; Ghrab *et al.*, 2014; Castle *et al.*, 2016)] and biotic [e.g., fungal and bacterial pathogens, virus and virioid diseases, insect and nematodes (Mudge *et al.*, 2009; Shokrollah *et al.*, 2009; Roistacher *et al.*, 2010; Louws *et al.*, 2010; Castle *et al.*, 2016)]. Furthermore, rootstock can theoretically affect every characteristic of the scion [e.g., overall plant growth, plant shape, fruit shape, fruit weight, fruit color, fruit firmness, content of phytochemicals in fruits and juices and postharvest storability and shelf life of fresh fruits (Ritenour *et al.*, 2004; Roupheal *et al.*, 2010; Orazem *et al.*, 2011; Turhan *et al.*, 2011; Castle *et al.*, 2016)]. In applied horticulture, all these factors play a determinant role for the final choice of the best rootstock/s for each one given grove having its own particular characteristics.

Although there are thousands of research papers describing the special effects of various rootstocks on

agronomical, phytosanitary, phenotypical, morphological, anatomical, physiological and biochemical aspects of scions, belonging to a wide range of plant species, the implicated mechanisms are still quite obscure and need to be elucidated in the future. Recently, Aloni *et al.* (2010) and Goldschmidt (2014) reported that long-distance protein, mRNA and small RNA graft-transmissible signals currently emerge as novel mechanisms which regulate nutritional and developmental root/top relations and may play a crucial role in investigating basic processes in rootstock-scion communication. They further noted that available molecular tools (e.g., gene silencing) today are expected to advance our understanding and eventually resolve the long standing grafting mysteries, relating mainly to the interactions of each rootstock-scion combination (Aloni *et al.*, 2010; Goldschmidt, 2014). Apart from that, anatomical, physiological and genetic basis for compatibility between each rootstock-variety combination need to be examined in a wider biological context (Mudge *et al.*, 2009). Undoubtedly, such studies are easier to be carried out with herbaceous vegetables or some plant models, compared to fruit and ornamental perennial trees. The very short biological cycles of vegetables and other species used widely as model plants offer the opportunity to researchers to investigate the effects of rootstocks on all critical vegetative and reproductive growth stages of plants, including studies not only at genetic, but also epigenetic level. In any case, breeding, selecting and testing of new rootstocks with desirable attributes will greatly benefit from the understanding of how exactly the rootstocks can affect the growth and development of scion. However, since the results from several horticultural plants may not be applicable to other species, research on species-specific grafting responses is required. Moreover, given that most of the published papers present the response of grafted plants to only a single stress, in the absence of any other biotic or abiotic one, the question remains whether the concurrent imposition of two or more stresses alters dramatically the specific responses of a rootstock to each stress separately. Towards acquiring a better knowledge concerning the rootstock-scion interactions, every scientific paper about basic and/or applied research on the rootstocks is well-welcome for publication, after rigorous peer review process, to the American Journal of Agricultural and Biological Sciences (AJABS).

Overall, each rootstock is a multi-dynamic horticultural tool functioning as a bridge, *i.e.*, as an artificial Trojan horse, by which a cultivar with important agronomical traits can be ideally cultivated to a farm with too specific unfavorable environmental, phytosanitary and/or cultural management conditions. Actually, the use of appropriate rootstocks increases the tolerance of cultivated varieties under adverse biotic and abiotic conditions. Rootstocks can further affect

significantly the overall behavior of scions, including specific growth characteristics, yield efficiency and the main quality indices of horticultural products. As a result, the production of quantitatively more and qualitatively better agricultural products and by-products can be achieved by using suitable rootstocks. From a practical point of view, the choice of the most appropriate rootstock (s), for a given farm, variety and cultural management conditions, is considered as an environmentally friendly and sustainable farming practice lowering the use of agrochemicals (e.g., pesticides, fertilizers) and other costly inputs (e.g., water). It also helps in protecting the environment, the consumers and the farmers, *per se*, but also in decreasing the production costs and in increasing the overall farm's profitability. Except for the conventional farms, the role of rootstock is undoubtedly vital under conditions of sustainable, integrated and organic, farming. Concluding, the unique value of rootstocks as key factors for the successful cultivation of horticultural crops is unquestionable, rendering them timeless allies for farmers growing vegetables, grape vines and/or fruit trees.

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