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Rootstocks and Grafting of Tomatoes, Peppers and Eggplants for Soil-borne Disease Resistance, Improved Yield and Quality

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ABSTRACT

Grafting of the Solanaceae is an environmentally friendly operation which reduces the incidence of crop infection by soil-borne diseases and reduces the population of soil-borne pathogens in a similar way to the application of crop rotation. Selection and use of highly compatible rootstocks, with resistance to soil-borne diseases and nematodes, allows the cultivation of high quality cultivars which otherwise would be sensitive to infested soils. Production of these cultivars is demanded by the consumers, so grafting enables favorable competition both for conventional and organic farming. Moreover, grafting protects the grower from exposure to harmful chemicals used for soil sterilization, and the consumer is protected from their residues.

Keywords: grafting, rootstocks, damage, nematodes, resistance, soil-borne pathogens
Abbreviations: **EU**, European Union; **IPM**, integrated pest management; **MB**, methyl bromide; **RH**, relative humidity **TMV**, tobacco mosaic virus

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INTRODUCTION

The area of land that is suitable for the cultivation of vegetables is rather restricted and remains approximately constant from year to year. Because of the repeated cultivation of crops on the same land, rapid multiplication of soil-borne diseases occurs, resulting in an increasing number of crop infections by diseases, such as *Fusarium*, *Verticillium*, etc. These fungal diseases are characterized by the appearance of yellow-brown lesions on the leaves and blockage and discoloration of the vascular system, the function of which is obstructed, leading to wilting and ultimately death of the

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Invited Review

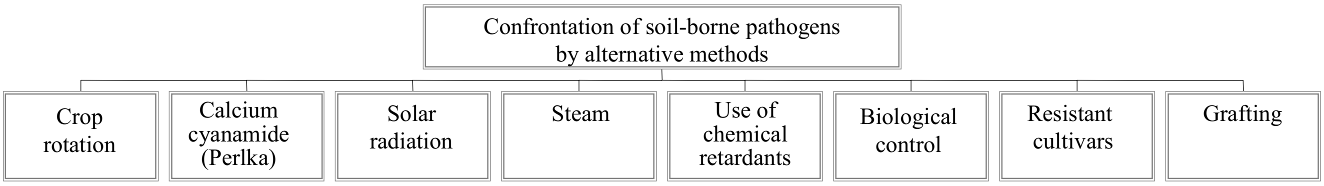

Fig. 1 Alternative measures to methyl bromide which can be used for the control of soil-borne diseases.

plant. In consequence, there is a loss of yield and income (Lee 1994; Oda 1995; Bletsos *et al.* 2003; Bletsos 2006). Until 2005, soil-borne diseases were controlled by soil fumigation with methyl bromide (MB). However, the use of MB has been suspended since 2005 in developed countries, and under the Montreal Protocol it is expected to be suspended in developing countries within the near future (Anonymous 1998) for the following reasons:

(a) It constitutes a health hazard for the users during application (Ristaino and Thomas 1997; Geoffrey *et al.* 1998),

(b) It increases the residues of Bromium (Br) in fresh produce to concentrations that are dangerous for the health of the consumers (Roughan and Roughan 1984),

(c) It causes pollution of the underground water (Warren *et al.* 1997), and

(d) It escapes into the atmosphere and has a negative effect on the ozone layer, resulting in an increase in the amount of ultra violet radiation which reaches the earth surface, and leading to an increased risk of skin cancer, eye disorders and crop damage (Robock 1996; Diffey 2004).

The restriction of MB for soil fumigation has a negative effect on the intensive cultivation of the Solanaceae on the same soil due to the fact that the cultivated cultivars and hybrids are sensitive to soil-borne diseases. Hence other methods of soil disinfestation must be adopted (**Fig. 1**).

Crop rotation restricts the spread of soil-borne diseases (Cirulli *et al.* 1990), but is difficult to employ for vegetable crops because the area under cultivation is more or less restricted and continuously in use every year. Additionally, the overwintering forms of these pathogens can survive for more than 20 years (Garber 1973).

Chemical control of diseases with calcium cyanamide (Perlka) is used in restricted areas (greenhouses) for the control of *Verticillium* on eggplant (*Solanum melongena* L.) (Bletsos 2006).

Solar radiation, as described by Katan *et al*. (1976) in Israel, is applied with satisfactory results for the control of *Verticillium* on tomatoes (*Lycopersicon esculentum* Mill.) (Morgan *et al.* 1991), or *Verticillium* and *Fusarium* on potatoes (*Solanum tuberosum* L.) and eggplants (Melero *et al.* 1989; Morgan *et al.* 1991; Bletsos *et al.* 2002). This method is not used extensively because at the time that temperatures are high enough for application, crops are still being grown.

Steam is highly effective, but expensive to apply and requires specialized, high-cost equipment.

The use of chemical growth retardants has not had encouraging results with respect to fungal pathogens (Tjamos *et al.* 1981).

Biological control using fungi (*Talaromyces flavus*) or bacteria (*Bacillus* sp.) is still under experimentation and evaluation (Tjamos and Velios 1997).

The use of resistant cultivars offers a satisfactory solution for the control of some soil-borne diseases. With resistant cultivars it is possible to improve yield and quality through ‘environmentally-friendly’ procedures that require a low input from the grower and therefore reduces the cost of production (Johnson and Jellis 1992). The production of resistant cultivars by selection within the cultivated crops is difficult because of the low degree of genetic diversity (Kaloo 1993), whereas the transfer of genes to cultivated crops from wild species, many of which possess resistance to soil-borne pathogens, poses a number of difficulties (Bletsos *et al.* 1998); moreover, the resistance may break down as new strains of the disease appear (Nicklow 1983; Kaloo 1993). In general, the selection for resistance requires many years of work, and there is always the danger of inducing new, resistant strains of pathogens.

Grafting of cultivated vegetable plants on to wild, resistant species is a method which is both practical in its application and ‘environmentally friendly’, but above all it offers the grower the possibility to grow pathogen-sensitive cultivars that have good quality traits and are in demand in the market (Lee 1994; Oda 1995; Bletsos *et al.* 2003).

GRAFTING HISTORY

Grafting is a technique through which the shoot parts of two different plants of the same or different species are physically joined together and subsequently grow as a single plant (Janick 1986).

Aristoteles (384-322 BC) and Theophrastus (371-287 BC) referred to the use of grafting, while during Roman times, fruit trees were grafted on a commercial scale, and St. Paul in a letter to the Romans refers to the grafting of the olive tree (*Olea europaea* L.) (Hartmann *et al.* 2002). Although grafting was applied mainly to tree crops, Chinese growers were grafting marrows (*Cucurbita moschata* Duch.) on to marrows (autografting) from the 5th century AD and the Koreans from the 17th century, so as to produce big marrows or pumpkins, which were used to store rice.

The first reference to heterografting (i.e. the grafting of two different species) concerned the grafting of watermelon (*Citrulus lanatus* [Thunb.] Matsum. and Nakai.) on to marrow at the beginning of the 1920s by Japanese growers (Ashita 1927). From the early 1930s, and subsequently, Korean and Japanese growers applied grafting commercially to watermelons on Lagenaria (*Lagenaria siceraria* (Mol.) Standl.) rootstocks (Lee 1994). Eggplant was grafted for the first time on *Solanum integrifolium* Poir. during the 1950s, followed by tomato during the 1960s. From 1960-1970, grafting has been commercially applied to watermelons, cucumbers (*Cucumis sativus* L.), melons (*Cucumis melo* L.), tomatoes, eggplants and peppers (*Capsicum annuum* L.) (Oda 1995, 1999).

Early on, Korean growers grafted seedlings when they were already large and the success rate was <50% (Ashita 1930 and 1934). In addition, a worker was able to graft only 150 seedlings per day. Subsequently, seedlings were grafted at an early stage of development, and to keep the graft in place, moist straw or paper was used; with this method workers could graft 800-1200 seedlings per day. Today, the rootstock and scion are held in place by various types of plastic clips and one worker can graft more than 1500 seedlings a day, whereas a robot can graft over 10,000 seedlings a day.

The discovery of polyethylene film and its application to agriculture from the beginning of the 1960s facilitated the rapid production of seedlings in plastic-covered greenhouses and helped to establish commercial enterprises for the production and distribution of grafted vegetable seedlings. Scientific research for the discovery and creation of new rootstocks was intensified towards the end of the1960s, and in the same decade the percentage of grafted vegetables (watermelon, cucumber, melon, eggplant and tomato) under commercial production rose to 59% of the total area under cultivation in Japan and 81% in Korea (Lee 1994).

In Europe, vegetable grafting started commercially from the early 1990s, initially in response to the need to grow produce without residues, but more recently because of the restrictions imposed on the use of MB for soil fumigation and the increase in demand for vegetables grown under IPM and organic systems.

In the USA, growers engaged in organic farming have recently started to graft vegetables to reduce infection from soil-borne pathogens and nematodes. In the developing countries of America, (e.g. Mexico and Guatemala) projects are being financed by the UN to explain to growers the advantages of grafting vegetables and how to do it.

In Greece, grafting was first carried out with watermelon during 1970-1980 and today grafting is commercially used for 90% of all watermelons, 30% cucumbers, 20% melons, 20% tomatoes, 15% eggplants and 10% peppers. The production and distribution of grafted vegetable seedlings is carried out by modern commercial enterprises, which buy rootstocks for grafting from relevant seed producers.

GRAFTING TECHNOLOGY

The grafting of vegetables is a technical procedure that is carried out manually or with the aid of special equipment (simple machines or robots). The following steps are involved:

(a) Selection of the rootstock and scion,
(b) Application of the selected grafting method,
(c) Healing of the wounded cut surfaces,
(d) Evaluation of the grafting success,
(e) Acclimatization (hardening) of the grafted seedling under suitable environmental conditions so as to become strong enough to withstand the shock of transplantation, e.g. to the field or greenhouse.

For tomato in Greece, seeds of the rootstock and scion are sown in trays (65 × 33 cm, with 128 individual cells per tray). After grafting, the seedlings are held under cover for 6-10 days to heal, following which they are transferred to the greenhouse and held at 20/18°C (day/night). By 35-37 days from sowing, the grafted seedlings are ready for transplantation to the greenhouse or field (Bletsos, unpublished data). In some high technology nurseries, seedlings are grafted under aseptic conditions to avoid contamination with disease.

Selection of rootstock and scion

Suitable rootstocks for grafting vegetables are those with good compatibility, resistance to low temperature, soil pathogens (*Fusarium*, *Verticillium*) and nematodes, encourage good growth of the scion, increase production and do not reduce produce quality. These rootstocks belong to the same, or a related, genus or they are F_1 hybrids between related species. A good number of rootstocks with some of the above characteristics are found on the market. Growers have the ability to select the most suitable rootstock for the growing season they are interested in, the cultivation method that they are going to follow (greenhouse or open field), the soil and climatic conditions of the area and the cultivar(s) to be grown (Singh *et al.* 2004).

Grafting methods

Growers and commercial nurseries throughout the world produce and sell grafted seedlings of the Solanaceous vegetables using the following methods, based on grafting in the region of the hypocotyl or epicotyl (**Fig. 2**):

(a) Tongue approach grafting (**Fig. 2A**),
(b) Hole insertion grafting (**Fig. 2B**),
(c) Splice grafting (**Fig. 2C**),
(d) Cleft grafting (**Fig. 2D**),
(e) Horizontal-pin grafting (**Fig. 2E**), as well as other approaches.

During recent years, grafting in the hypocotyl region is preferred because when grafted in the epicotyl, lateral branches form from the region of the cotyledons and must be removed before the grafting seedlings are sent to the growers.

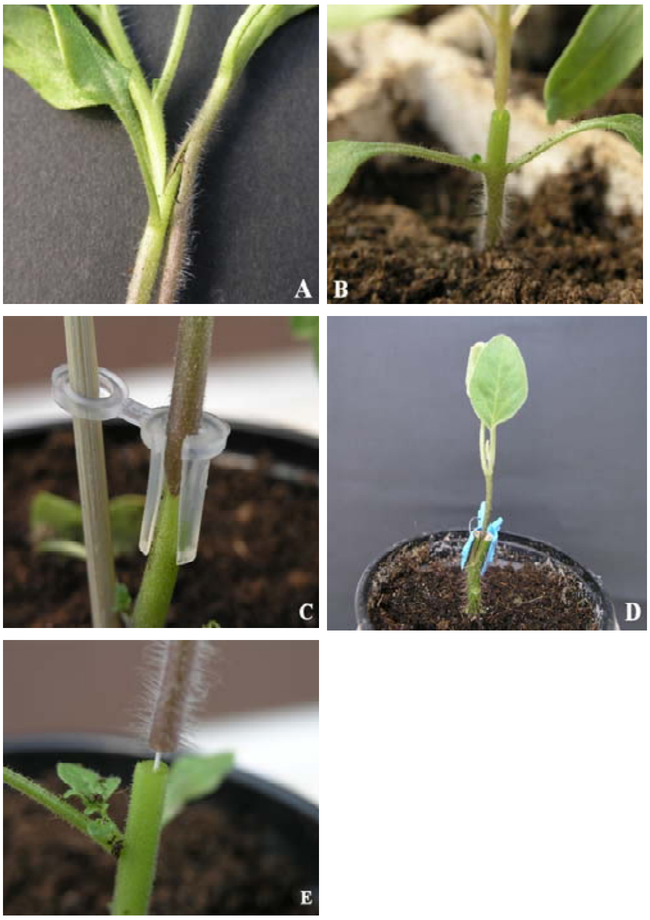

Fig. 2 Methods of grafting of the Solanaceae crops. (**A**) Tongue approach grafting, (**B**) Hole insertion grafting, (**C**) Splice grafting, (**D**) Cleft grafting, (**E**) Horizontal-pin grafting.

Tools, clips and grafting aids

Specially designed knives and hole-making equipment have been developed for use in manual grafting. To keep together the cut surfaces in contact after grafting, different accessories (e.g. clips of various types) are used (**Fig. 3**). For example:

(a) Simple plastic clips, with a circular metallic spring to open and close the clip, are used mainly with the tongue approach and splice grafting methods (**Fig. 3A**),
(b) Special elastic pipe-like clips made from silicon, with a splice to facilitate opening and closing with or without any other auxiliary accessories, are used to support the grafted seedlings in many nurseries and by growers who are grafting Solanaceous species manually or by robot (**Fig. 3B**),
(c) Smaller elastic, silicon-based, pipe-like accessories with a side splice are used for grafting small tomato, eggplant and pepper seedlings (**Fig. 3C**),
(d) Plastic clips for use by robots (**Fig. 3D**),
(e) Ceramic pins, which are very useful for grafting manually or by robot (**Fig. 3E**). These can also be used with self-adhesive tape and glue (Oda and Nakajima 1992).

The clips vary in size and shape, according to the manufacturer, are of low cost, easy to use for various shoot diameters and can be reused several times. Grafted plants can also be supported upright by special wooden or plastic sticks (**Fig. 3F**).

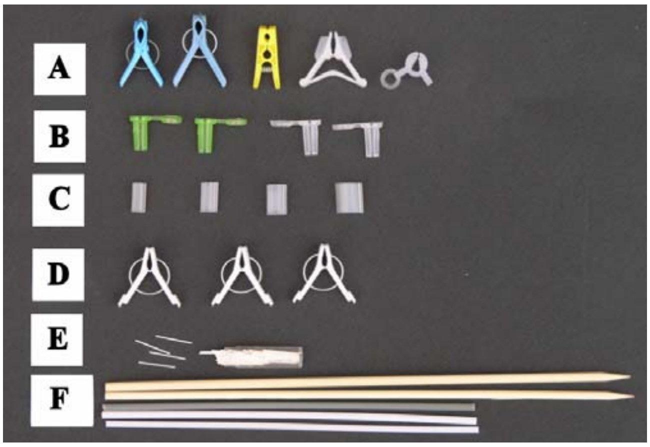

Fig. 3 Clips and supports of various types that are used for grafting vegetables. (**A**) clips used with the cleft method, (**B**) Pipe-like clips of silicon with a splice, (**C**) Pipe-like clips for grafting small size seedlings, (**D**) Clips for use by robots, (**E**) Ceramic pins, (**F**) Wooden and plastic sticks for the support of grafted seedlings.

Estimation of grafting success

Grafting is considered to be successful when a complete union of the vascular system of the rootstock and scion is achieved, allowing the unhindered transfer of water and nutrients from the rootstock to the scion and the transfer of photosynthates and growth substances from the scion to the rootstock. In small commercial nurseries with no specialized equipment, grafting success depends on the experience of the grower and the nursery personnel, and is assessed visually by the appearance of the grafted seedlings and the growth of the scion. In contrast, in modern, well-equipped commercial nurseries, the success of grafting is determined with methods such as:

(a) **Thermic cameras.** In successfully grafted plants, water is transferred smoothly from the root to the leaves of the scion where, due to transpiration, the temperature is 2-3°C lower than that of the leaves of the unsuccessfully grafted seedling. Intermediate leaf temperatures are recorded in the case of partly successful grafting because of the greater difficulty in water transfer in this case (Torii *et al.* 1992).

(b) **A vertical cut at the surface of the graft**. When tomato is grafted on to a tomato rootstock, the vascular system is connected directly. However, when tomato is grafted on to an eggplant rootstock, the vascular system of the tomato forms a curve above the grafted surface, and when grafted on to *Solanum torvum* Sw. this curve is even larger (Oda *et al.* 2005).

(c) **Measurement of the electric wave** transferred from the scion to the rootstock through the surface area of their connection. This transfer is related to the histological changes that occur during the union of the rootstock and scion. The electrical resistance between the rootstock and scion of grafted tomatoes is high for 2-3 days after grafting, due to the fact that during this time isolative tissue is formed and increases. Over the next 3-4 days the electrical resistance steadily declines as the formation of isolative tissue decreeses, and finally falls to zero (which is the value for non-grafted stems) as callus is formed (Yang *et al.* 1992). At this stage, complete union of the vascular systems of the rootstock and scion has been achieved, and in tomato the plant's hydraulic system becomes fully operational within 4-5 days of grafting (Turquois and Malone 1996).

Acclimatization

In modern commercial nurseries, grafting takes place in specially designed units where temperature, humidity and light are controlled so as to achieve maximum product quality.

The percentage of grafted seedlings that survive depends on the method of grafting which is applied, the conditions under which healing of the graft is conducted and the subsequent acclimatization (hardening) process. All these are important factors for the survival of the grafted plants when transplanted to the greenhouse or the open field (Oda 1999).

The method of acclimatization depends on the means at the grower's disposal. Denna (1962), who did not have any special means for acclimatization, used plastic bags to enclose the grafted seedlings so as to maintain high humidity until the union of rootstock and scion was complete. On a small scale, Bletsos (unpublished data) acclimatized grafted seedlings under inverted trays covered with transparent plastic, and the RH within was maintained at up to 100% by spraying with water. Similarly, commercial growers frequently use plastic covered tunnels in which the RH is maintained close to 100% level by sprinklers, while at the same time shading nets are employed to reduce incoming radiation, lower the temperature and light intensity, and thus reduce the incidence of wilting and accelerate healing (Nobuoka *et al.* 1997).

In modern commercial nurseries, the grafted seedlings are usually placed in trays of 50-70 seedlings each and transferred to specially constructed tunnels within which the temperature is maintained at 24°C and RH at 100%. The healing of the union of the rootstock and scion relates to air movement, light intensity and RH, and the grafted seedlings remain in these tunnels until the union is complete. Acclimatization is achieved by the gradual opening of the shading net and plastic cover (Nobuoka *et al.* 1997).

Care of seedlings before grafting

For successful grafting, it is important that the rootstocks and scions are of approximately the same size (height and diameter), depending on the grafting method to be applied. Seedlings (rootstocks and scions) are irrigated regularly, and are exposed to sunlight for 2-3 days prior to grafting. During grafting every effort must be made to increase the possibility for complete union of the vascular systems of the rootstock and scion (Oda 1995). For this, it is recommended to maximize the grafting surface and to keep the cut surfaces moist and in constant contact by the use of appropriate clips until the union is complete.

Care of seedlings after grafting

The care of seedlings after grafting refers mainly to acclimatization (as discussed above). If seedlings begin to wilt they must be immediately sprayed with water. The amount and duration of shading depends on the atmospheric conditions. More shading is needed during sunny days.

Micrografting

With the term micrografting we mean the grafting of meristomatic tissues *in vitro* in the laboratory in which the shoots of one plant are grafted on to the shoots or roots of another plant so as to combine the characteristics of the two plants. This method was used for the first time in 1952 by Morel and Martin for the production of virus-free dahlias. On a commercial scale, it is used for tree crops (mainly citrus) and the production of disease- (especially virus) free plants (Obeidy and Smith 1991).

Micrografting was initially used on vegetables to study the physiological basis of the grafting process and to determine the chemical basis of cell to cell union. Using *in vitro* grafting of internodes of tomato, *Nicandra physalodes* (L.) Scop. and *Datura stramonium* L. in various combinations (Jeffree and Yeoman 1983), it was found that pectins from the internodes of one species reduced the success of grafting, and in other combinations reduced the ability to form a common vascular system between rootstock and scion. With the use of ^{14}C-sucrose, it was found that the transfer of sucrose through the point of union began 5 days after grafting and increased gradually thereafter (Schoning and Kollmann 1995).

Micrografting of vegetables on a commercial scale started only recently in an attempt to reduce the high cost of production of grafted seedlings with classical methods. Much of the cost results from the high price of hybrid vegetable seed, while for micrografting, only a small number of seeds of the rootstock and scion are required. Several thousand transplants can be produced from the 2-3 week seedlings within a short period of time (Sarowar *et al.* 2003). These plantlets are genetically and phenotypically identical and true to type (Bhojwani and Razdan 1983). At the age of 3 weeks, the plants that are produced by micropropagation (rootstocks and scions) are grafted in the laboratory using one of the classical methods for grafting vegetables (**Fig. 2**).

The success rate of micrografting is relatively high (80–90%) for tomatoes (Grigoriadis *et al.* 2005). By combining micropropagation of vegetable rootstocks and scions with micrografting, the production of strong genetically-uniform seedlings on a commercial scale is ensured. However, the cost of micropropagation is still high due mainly to the need for manual labour, hence in the last few years an effort has been made to mechanize and automate the whole procedure.

A recent innovation is mass propagation in bioreactors (Akita and Ohta 1998; Konstas and Kintzios 2003), instead of propagation on solid substrates, because there is more accurate control of the propagation conditions, and the division and selection of plantlets in the substrate is carried out with special robots (Aitken-Christie *et al.* 1995; Gambley *et al.* 1997).

The gradual introduction of seedlings to the vegetable propagation trade so as to reduce the role of seed, in combination with the demand for certified seed from organized growers and nurseries to produce and sell a uniform, guaranteed product, will help to increase the adoption of micrografting for the production of grafted vegetable seedlings.

Simple grafting machines and robots

Grafting is a procedure that has a high labour demand, particularly in large commercial nurseries, which need to produce thousands of grafted seedlings in a short period of time. It is estimated that to graft 3,000 cucumbers, 42 man-hours are required, with 70% of this time being spent for the union of rootstock and scion (Kobayashi 1991). Although the filling of the growing plates with soil or a soilless substrate, seeding, irrigation, fertilizer application and the control of the environment in the greenhouses can be carried out and controlled automatically, the actual grafting of seedlings is largely carried out manually. The need to satisfy high demand, but at the same time reduce production costs, makes the adoption of mechanization for grafting a necessity.

Today several types of simple grafting machines or fully automatic robots are available on the Japanese and Korean markets which can graft the Solanaceous species with a high percentage of success (Hwang *et al.* 1999). These machines and robots can graft as many as 600–1200 seedlings $hour^{-1}$, compared to 150-180 seedlings $hour^{-1}$ by a specialized worker. The robots employ suitable computer programmes that can select, sort and graft uniform seedlings (Kurata 1994; Lee *et al.* 1998). Tomato (Oda 1995) and eggplant (Oda *et al.* 1997) grafted by robot produced similar yields to those of plants grafted by hand.

In Greece, commercial nurseries for the production of grafted seedlings face the problem of employing experienced labourers to graft thousands of seedlings over a short period of time. At present, however, although the cost for introducing a robot is not very high, only one nursery has installed such a machine, but in the very near future it is likely that more nurseries will adopt this procedure.

Production costs

Grafted seedlings are preferred by growers because although the cost of purchase is high, the specialist grafting work and the initial care of the grafted plants is avoided. In the USA, the cost of grafted seedlings is about the same as the cost of soil fumigation with MB, but grafted tomatoes produce 15% higher yield than self-rooted ones. However, beyond the cost of buying grafted seedlings, the cost of weed control must be added. According to Leonardi and Romano (2004), the cost of preparation of grafted seedlings is 3-5 times higher than that of self-rooted seedlings, while in Greece grafted seedlings cost 3 times more than self-rooted seedlings.

Transportation conditions

When grafted seedlings are destined for the local market, they are packed in cardboard boxes and transported to the grower by closed truck. The temperature inside the truck must be held at 13-15°C to avoid stress, since the outside temperature at that time may be low. Under these conditions, seedlings can travel for 4 days without damage.

Big nurseries that export grafted seedlings of the Solanaceae to other countries must deliver a huge number of seedlings on specific dates, which is not possible by grafting over a few days. Therefore, the grafted seedlings are held for 4-6 weeks in growth rooms, where the temperature and light intensity are low. Under these conditions, the rate of metabolism is reduced and the seedlings remain in a good condition. Seedlings can survive even longer if they are grafted on rootstocks that are resistant to low temperatures (Kubota 2003). Because the boxes are densely stacked during transportation, the RH inside the box is very high (~100%) due to transpiration, so there is a risk of disease. Temperatures during transportation must not be allowed to rise as this may adversely affect subsequent growth and flower induction (Kubota and Kroggel 2006).

GRAFTING PHYSIOLOGY

The physiology of grafted seedlings differs from that of self-rooted ones at all stages of their growth and development.

Graft compatibility

Compatibility in grafting depends mainly on the botanical relationship between the rootstock and the scion. Incompatibility and failure in grafting are two different things. With the term incompatibility, it is understood that in cases where grafting is expected to be successful there is a complete failure of the rootstock and scion to join, so there is no possibility of the grafted seedling to grow and there is premature destruction of the scion. With the term grafting failure, it is understood that the growth of the scion fails as a result of unsuitable environmental conditions or a lack of experience of the personnel. Physiological incompatibility can result from a failure of recognition of the cells of the scion by the cells of the rootstock, a failure of response between the cut surfaces of the rootstock and the scion, or the effects of growth substances or toxins (Andrews and Marquez 1993).

Graft union

The union of rootstock and scion in woody plants is achieved through the cambium cells, which multiply and increase in size. Callus is formed on the surface of the union by the interaction of the cambial cells of the rootstock and those of the scion. The cambium that is present compels the callus tissue to differentiate to form xylem and phloem (Janick 1986).

In vegetables, the wounded cells at the cut surfaces of the rootstock and scion that come into contact during grafting die and form a dead tissue that is absorbed during the subsequent processes. The living cells of the rootstock and scion extend into the dead zone to form callus, which assists their union. A new vascular cambium is differentiated from which xylem and phloem forms so as to unite the vascular elements of the rootstock and scion (Andrews and Marquez 1993).

Translocation of substances between rootstock and scion

In grafted seedlings the ability to absorb and translocate ions, as well as to translocate photosynthates, hormones, alkaloids and viruses, is affected by the type of rootstock and scion. Vegetables are mainly grafted on to wild species in order to gain the advantage of their well-developed root systems. The grafted seedlings can then absorb more water and more inorganic salts compared to the self-rooted ones (Masuda and Gomi 1984), in particular the macro-elements (P, N, Mg and Ca) (Masuda and Gomi 1984) and the micro-elements (Fe and B) (Zaiter *et al.* 1987).

Boron is a microelement, an excess or deficiency of which can seriously reduce the growth rate and production of tomato (El-Sheikh *et al.* 1971; Francois 1984). Deficiency in B usually occurs in wet areas, while excessive concentrations of B occur in dry areas. Severe symptoms of B toxicity are found in vegetable crops in Israel because there is not enough surface or underground water to irrigate the crops and water from biological processing of sewage, which contains high levels of B, is used. Grafted plants can withstand a deficiency or excess of B (abiotic stress) and give satisfactory production of good quality in this situation.

In addition, grafted seedlings have the ability to absorb inorganic ions from the soil when the soil temperature is very low (Tachibana 1982; Masuda and Gomi 1984) due to the role of specific enzymes (Ahn *et al.* 1999). The absorption and translocation of Ca by grafted tomatoes is affected by the environmental conditions (temperature, RH and light intensity) (Chung and Choi 2001), whereas Fe uptake is affected by the type of rootstock (Rivero *et al.* 2004).

The Solanaceae produce alkaloids, which are concentrated in the roots and upper parts of the plant (leaves, shoots, fruit). For this reason the wild Solanaceous plants that are to be used as rootstocks must be checked first to ensure that the alkaloids which are produced in the root system are not translocated to the fruit of the grafted scion. For example, it is well known that nicotine, an alkaloid produced in the root of tobacco, is transferred to the aerial parts of the plant through the xylem and becomes concentrated in the leaves, and when tomato is grafted on tobacco (*Nicotiana tabacum* L.), nicotine similarly becomes concentrated in the tomato plant (Dawson 1942). Other alkaloids which are synthesized in the roots are transferred to the scion, but may not be traced either because the concentration in the shoots and fruit is very low or because they are metabolized by the scion. Thus, saponine A and aculeatiside B are synthesized and accumulated to high levels in the roots of *Solanum aculeatissimum* sensu Schulz, non Jacq. in high levels. When *S. aculeatissimum* is grafted on to tomato rootstocks, a small quantity of saponine is found in the leaves and shoots, but it is not present in the roots of tomato. When tomato is grafted on to *S. aculeatissimum* rootstocks, saponine is concentrated only in the roots of *S. aculeatissimum*, indicating that saponine is formed mainly in the roots of *S. aculeatissimum* and is not transferred to the scion (Ikenaga *et al.* 1990).

During grafting of vegetables it is also important to take all the necessary precautionary measures to avoid contamination of the scion by possible viruses in the rootstock or *vice versa*, since tomato virus may be transmitted by grafting. Some of the serious viruses that are transmitted by seeds and are present in the seeds of the rootstock can destroy the grafted seedlings if the rootstock seeds are not first treated by dry heat to neutralize the virus.

Growth effects

As a rule, tomato on a disease resistant rootstock is more vegetative and productive than the self-rooted plant (White 1963), but some rootstocks reduce the growth and production of the scions. For example, tomatoes and eggplants grafted on rootstocks of *Datura patula* (Abdelhafeez *et al.* 1975) *Solanum sodomaeum* L. and *Solanum auriculatum* Ait. show less growth, lower production and smaller fruits compared to the self-rooted plants (Shackleton 1965). On the contrary, tomato grafted on *S. laciniatum* grows better and gives a higher yield over a longer time period on soils with a high water content compared to self-rooted plants (Shackleton 1965). Tomatoes grafted on eggplants generally show reduced growth and lower yields than self-rooted plants (Abdelhafeez *et al.* 1975), whereas some commercial rootstocks used for tomatoes like 'He-man' and 'Beaufort' increase the growth and yield of eggplants (Topoleski and Janick 1963).

Physiological disorders

Studies of physiological disorders and other undesirable characteristics that appear on the fruit of grafted plants and which can be attributed to the effect of the rootstock have so far been confined to the Cucurbitaceae.

Stress tolerance

Vegetables are also grafted because they can grow and produce satisfactorily when the soil temperature is either lower or higher than normal, under dry or wet soil conditions, or in saline soil. Rootstocks are selected according to the problem to be confronted.

For example, eggplants grow better at a soil temperature of 18-21°C when they are grafted on *Solanum integrifolium* Poir. or 'Taibyo' VF F_1 (*S. integrifolium* x *S. melongena*), rather than when grafted on *Solanum mammosum* L. When the soil temperatures are low, e.g. 12-15°C, they grow better when they are grafted on 'Torvum vigor' (*S. torvum*).

Tomatoes grow better at soil temperatures of 22-35°C when grafted on 'LS-89' (*L. esculentum*), whereas at low (10-13°C) and high soil temperatures they grow better when grafted on a rootstock resistant to soil pathogens and nematodes 'KNVF' (*L. esculentum* x *L. hirsutum* Humb. Bonpl.) (Okimura *et al.* 1986).

Flower formation

When some vegetable species are grafted, there are changes in the number and sex of the flowers that form. For example, grafting was found to favour the flowering of sweet potato (*Ipomoea batatas* (L.) Poir.), but it did not affect flowering in tomato (Coggins and Lesley 1968). To date there have been no reports that grafting affects the flowering of eggplant or pepper.

Fruit quality

In general, the rootstock influences the quality of the fruit produced on the scion. When tomatoes are grafted on to the three rootstocks of *Solanum* that are resistant to soil diseases, *S. sisymbriifolium* Lam., *S. torvum* and *S. toxicarium* Rich., the fruit of the scion have approximately the same concentration of soluble solids (°Brix) as those of the self-rooted plants (Matsuzoe *et al.* 1996), but when they are grafted on to *S. integrifolium* Poir., the fruit sugar concentration (°Brix) is higher (Oda *et al.* 1996). Harnett (1974), however, reported that tomatoes produced by grafted seedlings are of lower quality than those from the same non-grafted scion.

Induced resistance to diseases and insect pests

Often grafted vegetable crops become more resistant to diseases and insects. For example, when a sensitive scion is grafted on a resistant rootstock, the shoots that develop from the surface of the union may be multiplied asexually so as to produce resistant plants (Goffreda *et al.* 1990).

THE GRAFTED *SOLANUM* VEGETABLES

The fruit-bearing Solanaceae (tomato, eggplant and pepper) are grafted on a commercial scale in order to reduce infection by: (a) pathogens (*Verticillium dahliae*, *Fusarium oxysporum* f.sp *lycopersici* and *Pyrenochaeta lycopersici*) (Harrison and Burgess 1962; Bletsos *et al.* 2002, 2004; Bletsos 2006), (b) nematodes (*Meloidogyne* sp.) (Tzortzakakis *et al.* 2006), (c) bacteria (*Pseudomonas solanacearum*) (Matsuzoe *et al.* 1993a), and (d) to increase growth vigour and production (Abdelhafeez *et al.* 1975; Lee *et al.* 1998; Bletsos *et al.* 2002, 2003) and (e) increase tolerance to low and high temperatures (Okimura *et al*. 1986).

In Europe, interest in grafting tomato, eggplant and pepper on resistant rootstocks was stimulated by the prohibition of MB for soil fumigation (Daunay 2008). This has encouraged breeders to change from the search for cultivars that are resistant to soil-borne diseases and low temperatures and instead create resistant rootstocks for grafting. The improvement of these species is very effective because they have a large genetic diversity.

Tomato

Rootstocks

Although tomatoes were initially grafted on eggplant, during recent years they are usually grafted on tomato rootstocks, which are resistant or tolerant to soil diseases and nematodes, tolerant to low and high soil temperatures, give vigour to the scion, increase production and do not decrease the quality characteristics of the fruits (appearance, uniform colour, °Brix, etc.) (Harrison and Burgess 1962; Matsuzoe *et al.* 1993b).

Tomatoes that are grafted on rootstocks of *L. esculentum* take up B better (Brown *et al.* 1971) and tolerate high temperatures (Okimura *et al.* 1986), whereas those grafted on *L. hirsutum* are not infected by corky-root disease (Harrison and Burgess 1962). Tomatoes grafted on the hybrid *L. hirsutum* x *L. esculentum* are not infected by *F. oxysporum* f.sp *lycopersici* (Harrison and Burgess 1962) while those grafted on *L. esculentum* x *L. hirsutum* are not infected by corky-root disease (El-Sheikh *et al.* 1971; Francois 1984), *V. dahliae*, *F. oxysporum* f.sp *lycopersici* or nematodes and show tolerance to low and high temperatures (Okimura *et al.* 1986). The tomato rootstock 'Beaufort', which carries a Mi resistant gene, are infected by nematodes, but give satisfactory production in polluted soils; so they can be characterized as resistant (López-Pérez *et al.* 2006). However, although tomato rootstocks (especially interspecific hybrids), present resistance, the formation of new pathogenic races means that the efforts to create new rootstocks should be continuous (Daunay 2008). Tomatoes that are grafted on to *S. integrifolium* produce fewer fruit, but with increased °Brix (Oda *et al.* 1996), whereas those that are grafted on to *S. sisymbriifolium*, *S. torvum* and *S. toxicarium* are not infected by *V. dahliae*, *F. oxysporum* f.sp *lycopersici* or nematodes and can tolerate low and high temperatures to give fruits with the same °Brix as those from self-rooted seedlings (Matsuzoe *et al.* 1996). Tomatoes grafted on *S. mammosum* have the characteristic of being able to take up water under conditions where there is of lack of oxygen in the root zone (Weng and Chang 2004).

Over the last few years, commercial rootstocks and interspecific hybrids (*S. integrifolium* x *S. melongena*) of eggplant have been created that are suitable for wet soil conditions and show tolerance to bacteria and other soil pathogens (Mian *et al.* 1995).

Experimental results

Tomatoes grafted on tomato or eggplant rootstocks show satisfactory yields (Oda *et al.* 2000). Oda *et al.* (1996) cultivated tomatoes grafted on the tomato rootstock 'Hawaii 7998' and on the eggplant rootstock of S. *integrifolium* and observed that a grafting incompatibility exists with *S. integrifolium*, resulting in a smaller diameter of the rootstock than the scion. The *S. integrifolium* rootstock produced less root growth, and the tomato fruit were affected by blossom-end rot, were of lower yield and contained more sugars (°Brix) than those grafted on 'Hawaii 7998'. This results from inefficient union of the vascular bundles of the rootstock and scion and the poor root system, which causes a lack of water in the aerial plant organs.

Self-grafted tomatoes or tomatoes grafted on commercial rootstocks of tomato F_1 hybrids 'He-man', 'Eldorado', 'Beaufort', 'Primavera', 'Nova' and 'Packmore', were cultivated in soil that had been sterilized with MB and soil infected with *V. dahliae.* From the results, it was found that the grafted plants showed fewer symptoms of *V. dahliae* infection on the leaves and the plants were 20.3-45.6% taller than the self-grafted plants. In the infected soil, the grafted plants gave approximately the same marketable yield (early and total) as self-grafted tomatoes. The root system of the grafted plants was up to 34.2% larger than that of self-grafted tomatoes by the end of the crop, while fruit quality (°Brix, pH, locule number, pericarp thickness dry matter) was similar in both cases (Papadaki 2006).

Tomatoes grafted on the commercial tomato rootstock 'Maxifort' gave a higher yield under organic cropping, while those grafted on the tomato rootstocks 'He-man', 'Primavera', 'PG3' and 'Beaufort' gave higher production in the greenhouse and open field, and the fruit had the same quality characteristics as that from self-rooted plants (Maršić and Osvald 2004; Khah *et al*. 2006).

Tomatoes that are grafted on eggplant rootstocks have a larger leaf surface area, root and shoot dry weight than self-rooted plants and give higher yields at high temperatures. In the Mediterranean countries of Greece, Lebanon, Morocco and Spain, although the cost of production of grafted tomato seedlings is high, their cultivation is economically profitable (Bersi 2007). In Morocco, 95% of greenhouse tomatoes (by area) are produced on grafted plants because they are not infected by *F. oxysporum* f.sp. *lycopersici*, *F. oxysporum* f.sp. *radicis-lycopersici* or nematodes, coupled to which they tolerate low temperatures and give higher yields (Bersi 2007). On eggplant rootstocks they are not infected by bacteria (*Ralstonia solanacearum*) and perform better than self-rooted plants under wet soil conditions (Palada and Wu 2007).

Eggplant

Rootstocks

The eggplant has a dense, extensive root system and for this reason the rootstocks on which it is grafted should have a similar root system in order support the growth of the scion (Kato and Lou 1989). The type of rootstock should also offer resistance to the soil-borne diseases of the region in which it will be cultivated. In Japan and Korea eggplant has been grafted since the 1920s and therefore it is in these countries that most research for suitable rootstocks has taken place (Lee 1994).

Eggplant is grafted on a range of rootstocks. These include eggplant lines and hybrids which are resistant to *Fusarium* and bacteria (Yoshida *et al.* 2004), are not infected by *Phomopsis*, withstand wind damage (Gao *et al.* 2001) and produce fruit with uniform colour and firm flesh (Suzuki *et al.* 2004). Suitable *Solanum* species include *S. integrifolium* (i.e. *S. aethiopicum* L., Aculeatum group) which is resistant to *Fusarium* and bacterial wilts, and has good compatibility with eggplant (Yoshida *et al*. 2004), and interspecific hybrids, such as S. *integrifolium* x S. *melongena*, which combine the resistance of both parents (Mian *et al.* 1995).

In Japan, eggplant is usually grafted on *S. torvum* and *Solanum sanitwongsei* Craib. (Yoshida *et al.* 2004). Eggplants grafted on *S. torvum* and *S. sisymbriifolium* are not infected by bacteria (Mian *et al.* 1995) or *Verticillium* (Gao *et al.* 2001; Bletsos *et al.* 2003). Moreover, those grafted on *S. torvum* show increased photosynthesis, are not infected by *Leucinodes orbonalis*, are resistant to wind damage, tolerate low soil temperatures and give higher yields (Gao *et al.* 2001; Bletsos *et al.* 2003).

In the gene banks of the member states of the EU, many *Solanum* wild types, collected from various parts of the world (especially from tropical and subtropical regions), are maintained for the possibility of using them or their interspecific hybrids as rootstocks for eggplant grafting. Before the wild types of *Solanum* are used as rootstocks, they have to be evaluated for resistance to *Verticillium*, grafting compatibility and their effect on growth and production. Within the Eggplant Network Project ('EGGNET 2000-2005'), financed by the EU, 56 *Solanum* accessions (21 *S. incanum* L., 10 *S. viarum* Dunal., 9 *S. scabrum* Mill., 7 *S. pseudocapsicum* L., 3 *S. torvum*, and 1 each of *S. indicum* L., *S. sepicula* Dunal., *S. capsicoides* All., *S. linnaeanum* Hepper & P.-M.L.Jaeger, *S. sisymbriifolium* and *S. melongena* LF3-24) were evaluated for resistance to *V. dahliae*. From this evaluation, it was found that the seedlings of accessions belonging to *S. torvum*, *S. sisymbriifolium*, *S. linnaeanum*, *S. capsicoides* and *S. viarum* are resistant to *V. dahliae*, show vigorous growth and so can be recommended as rootstocks for eggplant grafting. The accessions of *S. scabrum* and *S. pseudocapsicum* also possess resistance to *V. dahliae*, but the former exhibits incompatibility and the latter shows weak growth, and therefore they are not suitable for grafting eggplant. Finally, seedlings of accessions belonging to *S. incanum*, *S. indicum* and *S. sepicula* are susceptible to *V. dahliae* and so cannot be recommended as rootstocks. Of the 49 accessions with compatibility, eggplant is grafted commercially on those that give good growth to the scion, tolerate soil pathogens and give the highest yields, namely:

(a) *S. torvum*, which is resistant to *V. dahliae* (Bletsos *et al.* 1997; Gao *et al.* 2001; Bletsos *et al.* 2003; Garibaldi *et al.* 2005), bacteria (Mian *et al.* 1995; Gousset *et al.* 2005), *F. oxysporum* f. sp. *solani* (Toe 1984), nematodes (Tzortzakakis *et al.* 2006), and the fruit of the grafted scion have approximately the same °Brix as the fruit from the self-rooted scion (Bletsos *et al.* 2003).

(b) *S. sisymbriifolium*, which is resistant to *V. dahliae* (Alconero *et al.* 1988; Bletsos *et al.* 1998, 2003) and nematodes (Tzortzakakis *et al.* 2006), and the fruit of the grafted scion have approximately the same °Brix as the fruit from the self-rooted scion (Bletsos *et al.* 2003).

(c) *S. aculeatissimum*, resistant to *V. dahliae* but susceptible to nematodes (Daunay and Dalmaso 1985).

(e) *S. capsicoides*, resistant to *V. dahliae*, *Pseudomonas solanacearum* and nematodes (Roberts and Stone 1981).

(f) *S. incanum* group C, resistant to *Pseudomonas solanacearum*, *Leucinodes orbonalis*, *Phomopsis rexans*, low temperatures and moderately resistant to *Verticillium* (Baksh and Iqbal 1978; Hebert 1985).

(g) *S. linnaeanum*, resistant to the virus Y, salinity, and moderately resistant to *Verticillium* (Bletsos *et al*. 2003), *Thielaviopsis* and *Colletotrichum coccodes*, but susceptible to nematodes (El Mahjoub 1979; Roberts and Stone 1981).

(h) S. *viarum*, resistant to *V. dahliae*, *Leucinodes orbonalis* (Lal *et al.* 1976), *Epilachna vigintiocto punctata*, *Phomopsis* (Kalda *et al.* 1977), nematodes (Sonawane and Darekar 1984) and low temperatures (Baksh and Iqbal 1978).

Eggplants grafted on interspecific hybrids *S. torvum* x S. *santwongsei* are not infected by bacteria, whereas those on S. *integrifolium* x S. *melongena* tolerate high temperatures (Okimura *et al.* 1986).

Today, most eggplants are grafted on S. *torvum*, a species of tropical and subtropical regions, with good compatibility, a strong root system and results in strong plants. In Greece, it grows in the summer, flowers in early September (short photoperiod) and produces fruit which mature the following summer. To produce seed, it can be cultivated under cover so that temperatures in winter do not fall below 15°C. A disadvantage of this species is a lack of uniformity during seed germination and slow initial growth of the seedlings (Ginoux and Laterrot 1991; Bletsos, unpublished data). The grafted seedlings may suffer from Mg deficiency at first, due to insufficient Mg uptake by the rootstock (Tachibana 1982).

In Europe, eggplants are also grafted on species of *Lycopersicon* and their interspecific hybrids (*L. esculentum* x *L. hirsutum*) which, apart from their resistance to soil pathogens, are tolerant to low soil temperatures and therefore recommended for early production (Ginoux and Laterrot 1991).

Experimental results

Eggplant scions grafted on eggplant rootstocks have increased leaf area, stronger root systems and produce higher yields than self-rooted plants (Daunay and Malet 1986). Better performance and yield of eggplant grafted on tomato rootstocks has been confirmed by Ioannou (2001), both in the greenhouse and the field (Khah *et al.* 2004). Grafted plants have a higher rate of photosynthesis (Tsiprakou *et al.* 2005), larger root and shoot biomass, better fruit set and a higher number of seeds per fruit (Tsiana *et al.* 2005). Eggplants grafted on S. *integrifolium* by robot gave higher yields than those grafted by hand (Oda *et al.* 1997), while eggplants grafted on rootstocks of *S. torvum*, *S. gilo* Raddi., *S. aculeatum* O.E. Schulz, *S. sisymbriifolium* and *S. khasianum* C.B. Clarke, and cultivated in soil infected with *V. dahliae*, were not infected by the fungus and the fruit were larger, with approximately the same °Brix as fruit from self-rooted plants (Dongxin *et al.* 2000).

Eggplants of the traditional Greek cultivar 'Tsakoniki' grafted on *S. torvum* were stronger, taller, produced more secondary shoots and gave 161.2% (early) and 41.6% more (total) marketable yield than self-rooted plants of the same cultivar. Also, in a comparative study of 'Tsakoniki' that was either self-rooted or grafted on *S. torvum* or *S. sisymbriifolium* and cultivated over two years (1998-1999) in soil that was fumigated with MB and soil infected by *V. dahliae*, it was found that the grafted plants were taller, produced a higher marketable yield (early and total) and larger fruit than the self-rooted plants in both the fumigated and the infected soil. The greater height and yield of the grafted seedlings was attributed to their better-developed root system, and even though the two wild types were infected by *Verticillium* the infection occurred to a much lesser extent than in the self-rooted plants (Bletsos *et al.* 2003). In other experiments, 'Tsakoniki' was self-rooted or grafted on *S. torvum* and grown in soil that was either fumigated with MB and calcium cyanamide (Perlka) or infected with *V. dahliae*. The grafted plants were taller, had thicker stems, better developed root systems and higher vegetative mass than the self-rooted plants. Moreover, early and total marketable yields were significantly higher than those of self-rooted plants in both soil (Bletsos *et al.* 2002).

Recently, 'Tsakoniki' was either self-grafted or grafted on 37 *Solanum* accessions, namely 6 accessions of *S. aethiopicum*, 4 of *S. incanum* group C, 2 each of *S. sisymbriifolium*, *S. linnaeanum*, *S. macrocarpon* L., *S. incanum* group C/D and *S. viarum*, and 1 each of *S. violaceum* Ort., *S. torvum*, *S. marginatum* L., *S. richardii* Dunal., *S. tomentosum* L., *S. cinereum* R. Br., *S. sessilistellatum* Bitter., *S. aculeatissimum*, *S. arundo* Mattei, *S. atropurpureum* Schrank, *S. capsicoides*, *S. cyaneopurpureum* De Wild., *S. erianthum* D.Don, *S. palinacanthum* Dunal., *S. pyracanthos* Lam., S. *renschii* Vatke. and S. *supinum* Dunal., or on the commercial tomato hybrid 'Beaufort, F_1. Plants were cultivated in MB-fumigated soil and soil that was infected by *V. dahliae*. It was found that the eggplants grafted on all the rootstocks were infected by *V. dahliae*, but those grafted on *S. torvum*, *S. sisymbriifolium*, *S. linnaeanum*, *S. viarum*, *S. aethiopicum* group Aculeatum, *S. aethiopicum*, *S. incanum* group C, 'Beaufort' F_1, *S. incanum* group C/D, *S. capsicoi-*

des, *S. atropurpureum* and *S. pyracanthos* tolerated the infections, enabling the scion to grow, produce higher early and total yields, and fruit with a similar or better total soluble solids content (°Brix) than the self-grafted plants. The accessions that were most sensitive to *V. dahliae* were *S. aethiopicum* group Gilo, *S. macrocarpon*, S. *incanum* group D = S. *lichtensteinii* Willd., S. *sessilistellatum*, *S. aethiopicum* group kumba, *S. tomentosum*, *S. cinereum*, *S. cyaneo-purpureum* and *S. supinum* (Bletsos, EGGNET project; Bletsos *et al.* 2004).

Fruit from 'Tsakoniki' grafted on S. *torvum* and S. *sisymbriifolium* and stored in a modified atmosphere for 17 days at 10°C had a lower vitamin C content, were less firm and scored lower on organoleptic characteristics than fruit from self-rooted plants, but their shelf-life was better (Arvanitoyannis *et al.* 2005).

The better growth of grafted eggplants has been attributed not only to stronger root growth but also to a higher production of cytokinins, which are transported to the scion (Honami 1977; Kato and Lou 1989). Because the same scion may perform differently on different rootstocks, evaluation of scion-rootstock interactions is necessary prior to commercial application (Romano and Paratore 2001). For example, Passam *et al.* (2005) found that eggplant cv. 'Delica' grafted on tomato rootstocks grew better and produced a higher yield than the same cultivar grafted on eggplant rootstocks or self-rooted.

Recently, it was found that in tomato rootstocks that are grafted with eggplant, the mode of gene expression is altered so as to cause morphological and physiological changes in the scion (Zhang *et al*. 2008).

Pepper

Rootstocks

Unlike tomato and eggplant, peppers are grafted only on peppers of the genus *Capsicum*, which are resistant to *Phytophthora capsici*, viruses (mainly TMV) (Beyries 1974; Yazawa *et al*. 1980), soil pathogens and nematodes (Morra and Bilotto 2006). Recently, interspecific pepper hybrids have been created for use as rootstocks, and these exhibit exceptional tolerance to *Phytophthora* and viruses (Lee and Oda 2003). Rootstocks with resistance to nematodes and good grafting compatibility with the cultivated cultivars can be created by selection within the genus *Capsicum* (Oka *et al*. 2004). However, attempts to graft peppers on *S. scabrum* and *S. gilo* (Bletsos, unpublished data), 7 *Solanum* species and 13 eggplant lines were unsuccessful (Tai *et al*. 2004).

Experimental results

Yazawa *et al*. (1980) grafted sweet pepper (*C. annuum*, cv. 'Shishito') on interspecific hybrids of *C. annuum* x *Capsicum chinense* Jacq. and found that the grafted plants were stronger, resistant to bacteria and more productive than self-rooted plants. Pepper hybrids 'Edo' and 'Lux' grafted on five commercial rootstocks ('Snooker', 'Tresor', 'RX360', 'DRO8801' and '97.9001') and cultivated in the greenhouse were 28-29% taller and produced 22-46% higher marketable yield than self-rooted plants, while fruit of both grafted and self-rooted plants had the same dry matter, °Brix and titratable acidity (Colla *et al*. 2008).

When peppers are grafted, genetic material is transportted from the rootstock to the scion via the vascular system, which causes certain morphological and physiological changes to the scion. Morphological changes include the formation of upright or pendant fruit, either several together at the same node, or singly (Yagishita and Hirata 1987; Ohta 1991), fruits with two instead of four lobes (Taller *et al.* 1998, 1999), dwarfism and plants with small leaves and fruit malformations (Hirata *et al.* 2003). Physiological changes include changes in fruit colour, e.g. yellow instead of red at maturity (Taller *et al.* 1998, 1999), a lower capsaicin content and changes in the °Brix (Yagishita *et al*. 1985, 1990; Hirata *et al.* 2003). These characteristics may even be carried over into the next generation via the seed.

Resistance to nematodes varies between different accessions and lines of *Capsicum* spp. (Di Vito *et al.* 1991, 1995), while nematode resistance occurs also in lines of *C. chinense* (Fery and Thies 1997; Thies and Fery 2000). When peppers were grafted on resistant rootstocks of *C. annuum*, *Capsicum baccatum* Jacq., *C. chinense* and *Capsicum frutescens* L. and cultivated in nematode infected soil, the grafted plants produced double the yield of non-grafted plants (Ros *et al*. 2002; Oka *et al*. 2004). The use of resistant rootstocks decreases the incidence of nematode infection and reduces the nematode population in soil to a similar level to that brought about by crop rotation (Thies and Fery 2002). However, if grafted rootstocks are grown in the same soil for a number of years, nematode populations increase and infection occurs (Ros *et al*. 2002). Although it has been reported that the resistance of *Capsicum* species to nematodes remains constant at soil temperatures of up to 38°C (Di Vito *et al*. 1995), others suggest that resistance ceases at soil temperatures above 32°C (Thies and Fery 2000).

Morra and Billoto (2006) cultivated peppers grafted on five rootstocks of *C. annuum* and found that the rootstocks 'Graffito' and 'Gc 1002' have good compatibility, do not affect scion growth or production, and are resistant to *Phytophthora*; in addition 'Graffito' is resistant to nematodes. In other studies, grafted peppers grown in the greenhouse and inoculated with *Phytophthora* or *F. oxysporum var. redolens*, produced higher yields than similarly inoculated, self-rooted plants (Piedra-Buena *et al*. 2007). By evaluating several pepper lines (*C. baccatum*, *C. frutescens* and *Capsicum chacoense* Hunz.), rootstocks have recently been identified that give increased production of sweet pepper scions under hot-wet and hot-dry seasons (Palada and Wu 2008).

CONCLUSIONS AND FUTURE PERSPECTIVES

The cultivation of grafted vegetables is an established practice which has been adopted in several Asiatic and African countries during the past decades and is becoming increasingly applied to horticulture in Europe and America.

The principal problems pertaining to the culture of grafted plants are the additional cost of rootstock seeds, manual work for grafting and the care of grafted seedlings, the lack of grafting experience and the possible occurrence of physiological abnormalities related to grafting. However, grafted seedlings are not infected by soil diseases and give earlier and higher production. They can be cultivated out of season, they have less need for fertilizers, irrigation and agrochemicals, and they can extend the harvest period. In addition, they enable the cultivation of desirable cultivars that are disease-sensitive and make the production of vegetables in sustainable and organic agriculture more competitive. Partial or complete exploitation of these advantages depends on the size of the agricultural enterprise, its degree of mechanisation and technology, the existing cultivation practices and a comprehension of the advantages and disadvantages of using grafted material.

There are still areas of research that require attention. For example, in the Solanaceae there has been no reported work on the physiological disorders that may be incurred as a result of grafting, or for example on the effect of grafting on flower formation and the flowering process. To date studies on these aspects of plant growth in relation to grafting have been confined to the members of the Cucurbitaceae.

Future expansion in the cultivation of grafted vegetables depends on the continued creation of commercially-available, resistant rootstocks, and the introduction of machines and robots for grafting. The increasing demand of consumers for vegetables that are free of dangerous chemical residues, that are cultivated in a more 'environmentally friendly' way (i.e. with fewer fertilizers, agrochemicals, less water etc.), and the increased production derived from the use of grafted plants make the products of ecological agriculture more competitive and increase demand.

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