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Performance of interspecific *Cucurbita* rootstocks compared to their parental lines

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ABSTRACT

Commercial cucurbits are commonly grafted onto interspecific *Cucurbita* hybrid rootstocks. The unproven paradigm is that hybrid rootstocks are more vigorous, resulting in better yields and high-level resistance. The objective of this study was to test the above hypothesis by comparing the performance of parental lines to that of derived F_1 hybrids as non-grafted *Cucurbita* accessions and as grafted melons, in experiments conducted in the greenhouse and in the field. The response to biotic stress was evaluated in with *Rhizoctonia solani* inoculated non-grafted *Cucurbita* parents and hybrids. In four out of the five hybrid–parent sets evaluated, susceptibility of the hybrid to *R. solani* was reduced or comparable to that of the parents. Grafted melon performance, expressed by plant development index, physiological wilt incidence and fruit yield, was evaluated in the field and in the greenhouse. Three hybrids out of the five tested in the field exhibited lower physiological wilt incidence than their parents. In three parent–hybrid sets, the male parent exhibited the worst rootstock performance and in one case, the male parent exhibited the lowest wilting. Fruit yield of grafted melons was highly correlated to wilt incidence. According to our results, the superiority of the hybrid over its parents and the benefit of the interspecific *Cucurbita* rootstock are not conclusive and varies among crosses and traits. The pathological, horticultural and economic benefits of this approach should therefore be further tested and reconsidered.

1. Introduction

Grafted vegetables mainly tomato (Lee et al., 2010) and cucurbits (Oda, 2002), have been cultivated in eastern Asia for decades, but their adoption in the Western world, including Europe, the Middle East, and the USA, has been slow, beginning about 20 years ago. The shift toward using grafted transplants was motivated by researchers and growers who were looking for alternatives to soil disinfestation with methyl bromide (Ristaino and Thomas, 1997; Cohen et al., 2000, 2007; Davis et al., 2008). In fact, the primary goal for using grafted plants is to avoid damage caused by soilborne pests and pathogens in situations where genetic or chemical approaches to disease management are unavailable (Lee and Oda, 2003; Louws et al., 2010). In addition, important horticultural characteristics, such as earliness and yield increase, can also be achieved using grafted plants (Davis et al., 2008). Grafted plants are often more tolerant to abiotic stresses such as cold temperatures (Schwarz et al., 2010), salinity (Colla et al., 2006a, 2006b; Edelstein et al., 2011), boron (Edelstein and Ben-Hur, 2005; Edelstein et al., 2007) and heavy metal toxicity (Savvas et al., 2010; Edelstein and Ben-Hur, 2012). Moreover, grafted plants can exhibit an increase efficiency on the use of nutrients (Colla et al., 2010, 2011) and water (Rouphael et al., 2008).

Cucurbits can be grafted onto rootstocks of the same species (intraspecific), e.g. melon on melon (*Cucumis melo*; Cohen et al., 2007), or watermelon on watermelon (*Citrullus lanatus*; Edelstein et al., 2014; Thies et al., 2015), or onto cucurbits from other species (interspecific) (Lee and Oda, 2003). Different cucurbits are compatible with lines of *Cucurbita maxima*, *C. moschata*, and *C. pepo* (Davis et al., 2008). However, in most cases, commercial cucurbits are grafted onto interspecific *Cucurbita* rootstocks produced mainly by crossing *C. maxima* with *C. moschata* (Karaagac and Balkaya, 2013). Despite interspecific rootstocks seed production is problematic and more expensive; the use of these seeds is more common

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The unproven paradigm is that interspecific hybrid rootstocks are more vigorous, resulting in better yields and higher levels of resistance.

There is consensus among researchers that grafting watermelons onto *Cucurbita* or *Lagenaria* species tends to increase vigor, fruit size and yield (Davis and Perkins-Veazie, 2005–2006; Alexopoulos et al., 2007). However negative effects on fruit quality often emerge in grafted melons and watermelons. This may result in fruit enlargement, shape deformation, or appearance of white fibers in the fruit heart (Edelstein et al., 2014). To overcome these obstacles, growers use less vigorous rootstocks or control the grafted plant's development by reducing nitrogen fertilization (Jung-Myung Lee, personal communication).

Based on the aforementioned problems with interspecific rootstocks (Karaagac and Balkaya, 2013), the overall objective of this study was to investigate whether the interspecific hybrids indeed are necessary or its possible to use selected elite *Cucurbita maxima* or *C. moschata* lines for grafting. To test the hypothesis under different climate and stress conditions, our specific objectives were to evaluate: (1) the development of non-grafted interspecific *Cucurbita* hybrids compared to their parents; (2) the susceptibility of the non-grafted interspecific hybrids and parents to infection by *Rhizoctonia solani*; (3) the response of melons grafted onto these interspecific hybrids and their parents to the phenomenon of physiological wilt (PW) under field conditions; (4) growth, yield and quality of melons grafted onto hybrids and their parents under greenhouse conditions.

2. Materials and methods

2.1. Germplasm

In in this study, 3 experiments have been conducted evaluating always the same 15 cucurbit accessions (Table 1.) from the *Cucurbita* seed collection of the Cucurbit Research Section in Newe Ya'ar, Israel. This set consisted of 5 interspecific hybrids (H) given the numbers 516, 542, 604, 609 and 634, and the corresponding parental lines. These hybrids are crosses between *C. maxima* used as the female parent and *C. moschata* used as the male parent. Those interspecific Cucurbita hybrids were chosen because they have been tested in previous experiments in Israel and have successfully grown.

2.2. Evaluating the potential of the non-grafted Cucurbita accessions

2.2.1. Growth characteristics

Seeds of the 15 accessions were sown at two locations: Experiment 1 in a field located at the Newe Ya'ar Research Center (58% clay, 23% silt, 19% sand, 2.1% organic matter, pH 7.1). The field experiments consisted of 40 plants, with 4 replicates (10 plants per accession), with within-row spacing of 40 cm. The bed centers were 190 cm apart. Mean daily air temperature in the field ranged from 15 °C at night to 38 °C during the day, and daily soil temperature ranged from 26 °C at night to 32 °C during the day. Experiment 2 was conducted in a greenhouse in 10-L pots filled with sandy soil (11% clay, 4% silt, 85% sand, pH 7.8), with 4 replicates and 20 plants per accession. During the experimental period, greenhouse mean daily air temperature ranged from 17 °C at night to 46 °C during the day, and daily soil (depth 10 cm) temperature ranged from 18 °C at night to 49 °C during the day. For both experiments standard cultural practices for local commercial cultivation, including drip fertigation, were employed. One month after sowing, plants were harvested, and roots were gently rinsed of sand with running tap water and dried on a paper towel. Fresh and dry shoot and root masses were weighed. Stem diameter was measured by a caliber meter.

Table 1
Identification of female and male parents of *Cucurbita* spp., and their hybrids used in this study. Group number represents the hybrid and both parents.

Female parent (*C. maxima*)	Male parent (*C. moschata*)	Interspecific hybrid	Group
PI-177367-3	PI-183258	516	1
PI-419138-4	PUR	542	2
PI-169470-2-2	59327−3	604	3
PI-162671-1-2	DUS	609	4
PI-169466-1-3	SEM	634	5

2.3. Response of cucurbita rootstocks to Rhizoctonia solani

The 15 Cucurbita accessions (5 interspecific hybrids and their corresponding parental lines; Table 1) were grown in 0.5-L pots filled with a commercial potting mix (Fruhstorfer Erde, Vechta, Germany) to the first true leaf stage. *R. solani* isolate AG-4 (collection of Stanly Freeman, ARO, Volcani Center, Israel) was used for plant inoculation (6–7 leaves). Each treatment consists of 10 plants with 4 replicates. Since the symptoms of the Rhizoctonia are very clear so we did not have un-innoculated plants and the comparison was between the responcses of the different accessions to the pathogen. A 10-mm agar disk with the pathogen was taken from a petri dish and placed on the lower stem of the tested plants. A necrotic lesion developed in the plant tissue 7–10 days after inoculation. The lesion size was estimated and ranked as degree of disease from 0 to 5 (0–no disease, 1–initial infection, 2–up to 20% of the stem rotted, 3–up to 60% of the stem rotted, 4–up to 80% of the stem rotted, and 5–entire stem diameter rotted). The degrees were used as an indication of the plant's response. The experiment was repeated.

2.4. Evaluating grafted melons in the field

2.4.1. Evaluating the response of grafted melons to physiological wilt (PW)

Melons (cv. Ra'anan, HaZera Seeds, Israel) were grafted onto the 15 *Cucurbita* accessions at Hishtil nursery (Ashkelon, Israel) using the splice grafting method (Lee and Oda 2003). Transplants were planted at the Zohar experimental station in Ein Tamar, northern Arava Valley, Israel (lat. 30°94′ N, long. 35°32′ E), on 13 Dec 2013. Each treatment (rootstock–scion combination) consisted of 20 plants, i.e., 5 plants with 4 replicates, with within-row spacing of 40 cm. The bed centers were 190 cm apart. Standard cultural practices for local commercial cultivation, including drip fertigation, were employed. In addition transplants were treated three times (3 weeks after planting, at flowering and at fruit set) during the growing season with the fungicide azoxystrobin to prevent *Monosporascus cannonballus* vine decline and other soilborne diseases (Pivonia et al., 2010). The PW, expressed as the percentage of dead plants, was evaluated throughout the growing season. Fruits were harvested at maturity seven times during the growing season.

2.5. Evaluating growth and yield of grafted melons in the greenhouse

Melon grafted onto the same 15 *Cucurbita* accessions (Table 1) were transplanted into 10-L pots filled with a commercial potting mix (Fruhstorfer Erde, Vechta, Germany) on 23 June 2014 and cultivated in a 200 m^2 greenhouse at the Leibniz Institute of Vegetable and Ornamental Crops in Grossbeeren, Germany. During the experimental period, mean daily temperature was 27 °C ranged from 17 °C at night to 32 °C during the day. Mean relative humidity amounted to 63.0 and 80.5% during the day and night, respectively.

Mean daily photosynthetic active radiation in the greenhouse was 26.2 Mol m^{-2}. Each rootstock accession consisted of 2 plant in 4 replicates. Plants were daily irrigated until substrate in the pots was fully saturated with water. Additionally, plants received nutrient solution based on the recipe of Sonneveld and Straver (1994) during the week to provide them with sufficient. Plant development index as a measure of vigor was evaluated, ranked from 0 (bad) to 100% (good). Upon ripening, fruits were harvested and weighed.

2.6. Statistical analysis

The broad-sense heritability (h^2), which is $\sigma^2_{Genetic}/\sigma^2_{Genetic+Environmental}$ where σ^2 is the variation, was calculated for each trait using the “fit model” function. Genotype was defined as a factor with random effect and the genetic variation was calculated as percentage of the total variation (genetic + environmental). All traits were subjected to two-way ANOVA where the tested factors were: 1. Group (Hybrid + 2 parents); 2. Genotype (parent or F_1) and 3. Interaction (Group x Genotype). Entry means were compared using Tukey HSD and in some cases by Student's *t*-test to determine statistical differences between treatments ($P < 0.05$) using JMP software (SAS Institute Inc., Cary, NC, USA).

3. Results

3.1. Trait variations and heritabilities

All *Cucurbita* groups in this study (hybrid + 2 parents) were phenotyped both as non-grafted plants and as rootstocks for grafted melons. Trait are listed and basic statistics for the measured traits are presented in Table 2. There was a significant genetic effect for all traits, expressed as differences across lines and between parents and their F_1 hybrids (Table 2). Broad-sense heritability values, which is the ratio of total genetic variance to total phenotypic variance, ranged between 0.4 and 0.69. Rootstock and whole-plant trait heritability values were within the same range, indicating the importance of the rootstock effect on the measured traits.

3.2. Comparison between non-grafted Cucurbita parental lines and interspecific hybrids

3.2.1. Shoot and root growth

Root biomass (Fig. 1A), was affected interactively by the group and the genotype. The *C. moschata* parent had higher root biomass than the *C. maxima* parent in three out of four groups where both parents were included (2,3,4). In group 5, the C. *maxima* parent had significantly higher biomass than both C. *moschata* and the F_1 hybrid. The F_1 hybrid was not significantly different from the lower parent in any of these four groups, showing a surprising under dominance and obviously no heterosis. For shoot biomass (Fig. 1B), the group effect was not significant ($P = 0.18$), the genotype effect was significant ($P = 0.013$), and the interaction between them was not significant ($P = 0.099$). A significant difference between genotypes was found only within the group 5, where the *C. maxima* parent had significantly higher shoot biomass than both the *C. moschata* parent and the F_1 hybrid. Overall, an underdominance pattern was observed for this trait as well. For stem diameter (Fig. 1C), a similar pattern of either no difference between genotypes within a group or a trend toward underdominance was observed.

3.2.2. Response of cucurbita genotypes to R. solani

A significant interaction was found between genotype and group as there was no consistent superiority of parents from one species over those of another species, and the hybrids ranged all the way from over- to underdominance (Fig. 1D). In four out of the five groups evaluated, the hybrid was either less susceptible than the parents or showed an equivalent response. The exception was group 3, in which the hybrid was significantly more susceptible than both parents. Based on these results, the disease response or inheritance of resistance to *R. solani* varies across different accessions.

3.3. Analysis of Cucurbita rootstock performance using grafted melons under field conditions and in the greenhouse

A high and significant correlation was observed between PW (physiological wilt) and yield ($r = -0.85$) in the field experiment, suggesting that the observed yield variation can be mostly explained by tolerance to PW. This correlation was also evidenced by the two-way interaction plots for PW and yield, which showed the same pattern (Fig. 2A and B). A significant interaction was found between genotype and group for both PW and yield. In contrast to the experiment with the non-grafted accessions, here, as rootstocks, the interspecific F_1 hybrids were either between or better than their inbred parents. However, in none of the cases was F_1 significantly better than the best parent and therefore, here again, best-parent heterosis was not detected.

Fruit yield and plant development index (vigor) of the same grafted sets was evaluated in the greenhouse (Fig. 3). Significant interaction was found between genotype and group for both traits. For fruit yield, F_1 hybrids did not show any consistent pattern relative to the parents, with hybrid performance ranging between additive and dominant. For the plant development index, the interspecific F_1 hybrids were generally equal to or better than their inbred parents. However, with the exception of group 2 where the F_1 hybrid was significantly better than the best parent, the difference between the F_1 hybrid and best parent was not significant.

4. Discussion

The approach to breeding rootstocks of *Cucurbitaceae* is different from traditional plant breeding. With common vegetables, for instance, the breeder can see the plant and the fruit throughout the breeding process and direct the crossing toward the desired traits and the target of the program. However, the important functional organ of the *Cucurbita* rootstock is the root; the shoot and the fruit have no relevance to rootstock performance. Since information about root system performance and its contribution to the scion is very limited, breeders and growers have to depend on instinct when selecting promising rootstocks. They are usually looking for big, strong and vigorous rootstocks. In addition many rootstocks are selected based on disease resistance to plant pathogens and not just considering vigor. (Crino et al., 2007). The most common rootstocks for cucurbits are the interspecific hybrids between *C. maxima* and *C. moschata*, and rootstock breeding is performed mostly in China, Japan and Korea. In fact, most of the rootstocks used in the western world are imported from the Far East (Davis et al., 2008; Karaagac and Balkaya, 2013). It is unknown, however, whether rootstock breeding was constructed on random crossing of *C. maxima* and *C. moschata* accessions or based upon certain traits of the parental lines. Even if the latter is true, a rootstock developed in Japan or Korea will not necessarily be suited the hot climate of the Mediterranean basin, for example, the production area for most of the cucurbits consumed in Europe.

Although prevention of disease damage is the main motive for using grafting, precise knowledge of the response of *Cucurbita* accessions to many pathogens is lacking. Since the fungus *R. solani* attacks a wide range of plant species, including cucurbits (Sloane et al., 1983; Aegerter et al., 2000), and causes significant damage (Grosch et al., 2015), it was selected in the current study as

Table 2
Trait description and statistics across the five hybrid groups.

Trait	Experiment	Mean	Range	Broad- sense heritability
Cucurbita (non-grafted), root biomass (g)	Greenhouse	204.2	30–800	0.62
Cucurbita (non-grafted), shoot biomass (g)	Field	308.7	54–625	0.65
Cucurbita (non-grafted), stem diameter (mm)	Greenhouse	15.0	10–21	0.68
Cucurbita (non-grafted), *Rhizoctonia* severity (0–5)	Greenhouse	2.5	0–5	0.4
Grafted melons, physiological wilt (%)	Field	53.0	0–100	0.63
Grafted melons, yield (kg/plot)	Field	25.5	0–58.87	0.69
Grafted melons, fruit yield (g/plant)	Greenhouse	1530	0–4721	0.45
Grafted melons, plant development index (%)	Greenhouse	45.2	0–80	0.5

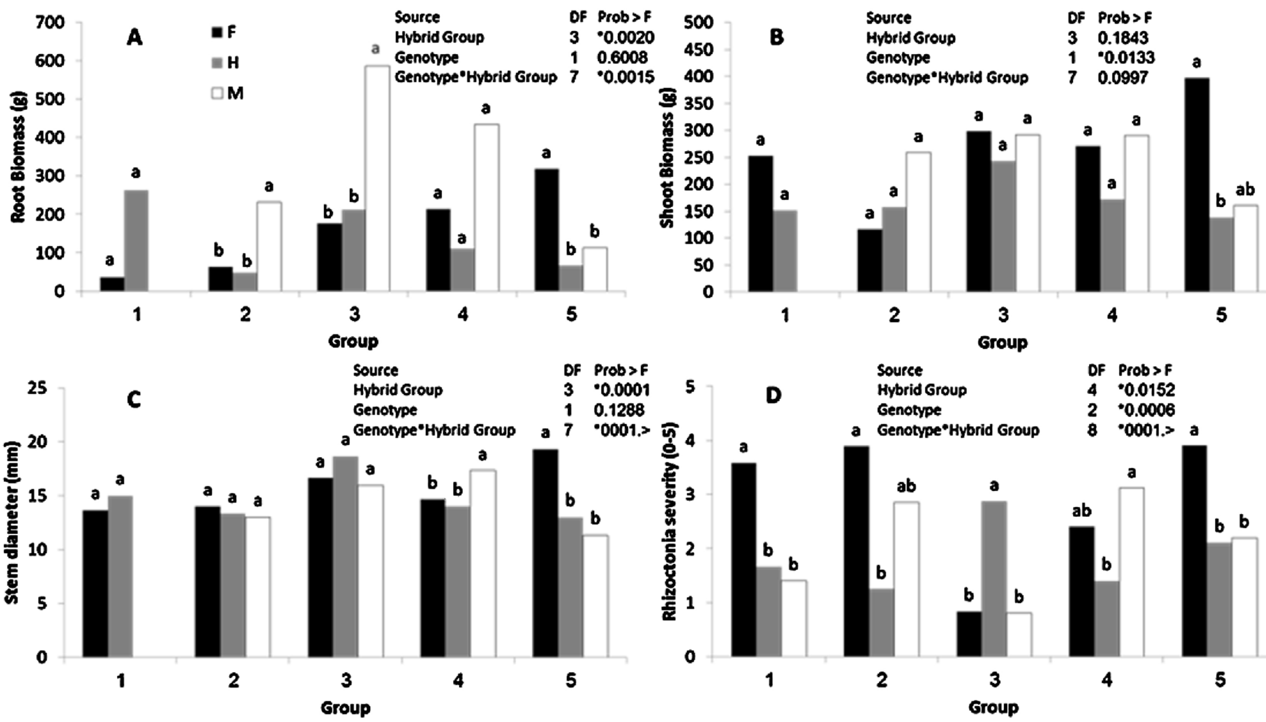

Fig. 1. Two-way interaction plots between genotype and group (Greenhouse Newe Ya'ar).
Characteristics of the *Cucurbita* rootstocks. **A.** Root biomass. B. Shoot biomass. **C.** Stem diameter. **D.** Response to infection with *Rhizoctonia solani*. On the X axis are the different groups (Table 1). For each group, mean performances of male (M), female (F) and hybrid (H) are plotted. Genotypes within the same group with different letters are significantly different at $P < 0.05$. In the right upper corner of each box are the statistics of two-way ANOVA. DF – degrees of freedom

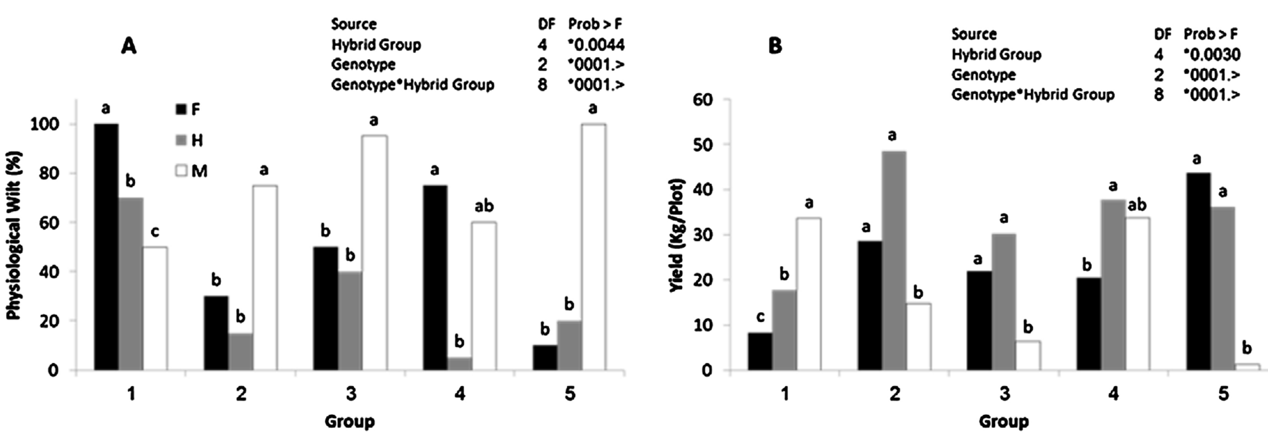

Fig. 2. Two-way interaction plots between genotype and group (Field Arava Valley).
Performance of grafted melon plants under field conditions. **A.** Field physiological wilt and not collapse (PW). **B.** Fruit yield. On the X axis are the different groups (Table 1). For each group, mean performances of male (M), female (F) and hybrid (H) are plotted. Genotypes within the same group with different letters are significantly different at $P < 0.05$. In the right upper corner of each box are the statistics of two-way ANOVA. DF – degrees of freedom

the model pathogen to demonstrate the variation in responses of *Cucurbita* accessions to pathogens, and to assess the parents' contribution to the hybrid's performance. Differences between the hybrid and its parents were evident. Low disease severity was recorded in

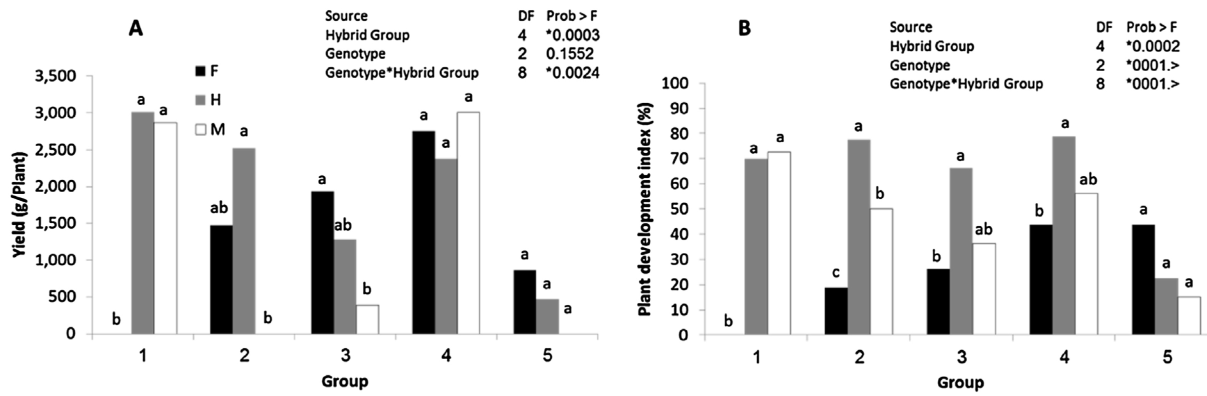

Fig. 3. Two-way interaction plots between genotype and parent–hybrid group (Greenhouse Grossbeeren).
Performance of grafted melon plants under greenhouse conditions. **A.** Fruit yield. **B.** Plant development index. On the X axis are the different groups (Table 1). For each group, mean performances of male (M), female (F) and hybrid (H) are plotted. Genotypes within the same group with different letters are significantly different at $P < 0.05$. In the right upper corner of each box are the statistics of two-way ANOVA. DF – degrees of freedom

H-609 (group 4 Table 1) and H-542 (group 2), but only the latter was significantly different from its two parents. The opposite reaction, in which the hybrid was significantly more susceptible than the parents, was exhibited by H-604 (group 3, Fig. 1D). These results provide additional evidence for variation existing in the germplasm, and for the need to gain precise knowledge toward rational breeding.

Agricultural heterosis (the superiority of the F1 hybrids over those of the parents) relates to hybrids that outperform their inbred parents with respect to yield. For most agriculturally important crops, commercial varieties are F_1 hybrids. The impact of heterosis on agriculture is widespread and it is estimated that globally, it has increased yield by 15–30% (Duvick, 2001). Interspecific hybrids are less common in crop breeding. While such hybrids can demonstrate extreme vigor compared to their parents (Robinson, 2000), in many cases they can suffer from incompatibility expressed as reduced fertility or even sterility (Chen, 2010). The use of interspecific hybrids has been shown to affect vigor or yield in various plant species (Goodspeed, 1933; Cheng et al., 2007; Albacete et al., 2015). For these reasons, interspecific hybrids can be attractive resources for rootstock breeding where vigor is an important trait, and the fertility of the hybrid or fruit characteristics are less important. In tomato, most of the commercial rootstocks for indeterminate varieties are bred as interspecific hybrids, providing resistance to soilborne diseases and increased vigor, thereby enabling long-term crops (Fernandez-Garcia et al., 2002; Black, 2003). While the role of heterosis in agricultural crops is not in question, the prediction of hybrid performance compared to parental lines is still a major challenge and a key objective in genetic research and plant breeding. All modes of inheritance can be found, and they vary across traits (Semel et al., 2006) as well as among crosses.

Although our sample size was limited, our data show that the interspecific hybrid concept does not guarantee a heterotic response. Thus, further research and breeding efforts are required to gain a better understanding of the variations in heterosis for rootstock performance across interspecific *Cucurbita* hybrids.

Although the production of interspecific hybrids of *C. maxima* and *C. moschata* is possible, it is often not easy to achieve. Thus, it is rather remarkable that Japanese breeders have produced, in some cases, seeds of interspecific hybrids with such efficiency that they could be marketed commercially. Their vigor is so exceptional that they are utilized as rootstocks for grafting cucumber, watermelon, and melon plants. A unique example of this success is the cultivar Tetsukabuto (Robinson, 2000). 'Tetsukabuto' was the first winter squash cultivar of a *C. maxima* x *C. moschata* interspecific cross. It was a cross of 'Delicious' (*C. maxima*) and 'Kurokawa No. 2′, an early cultivar of *C. moschata*. The success in producing seeds economically for this and some other *C. maxima* x *C. moschata* cultivars seems to be due to good combining ability (Robinson, 2000). 'Tetsukabuto' is used as a rootstock and its efficient seed production was probably one of the reasons that others began to follow the idea of using interspecific hybrids as rootstocks.

The PW of grafted melons that occurs in the Arava Valley of southern Israel in the early spring cropping is an example of a physiological disorder that is not related to pathogens. However, its exact cause is unknown. Trellised grafted muskmelons wilted short before harvest time, when the temperature is rising and the plants are loaded with fruit, in contrast to non-grafted melons or grafted plants grown prostrate (Cohen et al., 2007). The assumption, however, was that this was related to the quality of the rootstock–scion combination and to environmental conditions, such as high soil temperature or insufficient mineral uptake.

When evaluated under field conditions, no consistency was found with respect to PW. Three hybrids out of the five tested (Fig. 2A) exhibited less PW than their parents. The male parents exhibited the worst compatibility with the scion but in one case, the male parent gave opposite results, exhibiting the lowest wilting incidence. It seems that in three sets, PW and yield (Fig. 2B) of the surviving plants were closer to the performance of *C. maxima* rootstocks, used as the female parent. In two sets, with *C. moschata* used as the male parent, SEM (Table 1 group 5) and PUR (group 2) exhibited almost total incompatibility with the scion as most of the grafted melons collapsed shortly after transplanting.

The response of grafted melons to PW can differ under different conditions. The performance of the plant is the result of the roots' contribution to water and nutrient uptake, and hormone supply for long-distance signaling, which is a central aspect in the rootstock–scion interaction, including disease resistance (Guan et al., 2012). In the case of group 2 for example, it seems that the male parent made some contribution although its own rootstock–scion compatibility was rather poor. The hybrid plant's vigor in the greenhouse experiment was higher (albeit not always significantly so) than that of the two parents for group 4, 3 and 2 (Fig. 3**).**

It seems that today, most of the *Cucurbita* rootstocks are based on old stocks that originated from the Far East (King et al., 2010). The adaptation to Western conditions has been based on a trial and error approach. The creation of new rootstock cultivars is facing a lack of knowledge about the traits contributed by the roots, involving either differential uptake of water and nutrients or varying extents of molecular and hormonal long-distance signaling. The interspecific crosses can be beneficial in certain cases but should definitely not be the only approach taken. In other words, there is a need for rational breeding adapted to the requirements of particular areas and growing conditions. The success of interspecific hybridization between *C. maxima* and *C. moschata* is often limited. Seeds are frequently empty and the rest may have poor germination ability, thus making seed production uneconomical. One solution might be the approach taken by Karaagac and Balkaya, (2013). They selected parental lines based on plant vigor, hypocotyl diameter, seed yield and compatibility. Indeed, such a tactic can increase seed yield, seed quality and profitability of the seed producer. Nevertheless, it does not take the germplasm characteristics into account and may limit the germplasm's use, thereby reducing the genetic variation and the availability of desired traits. The community of grafting practitioners would gain from the development of a searchable and publicly accessible database that provides comprehensive information on disease resistance, biotic stress resistance, compatibility issues, sources of stocks, vigor effects and other important information. This would aid in technology transfer and allow grafting technologies to be better integrated into diverse production systems (Louws et al., 2010). A similar approach was taken by Ara et al. (2013) in an attempt to create a rootstock suitable for hot regions. They evaluated an interspecific inbred line of squash named 'Maxchata' for its photosynthetic attributes, compared to its parents *C. maxima* and *C. moschata*. C. moschata was found to have the best photosynthetic machinery for sustaining the heat regime, followed by 'Maxchata', while C. maxima was the most susceptible.

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