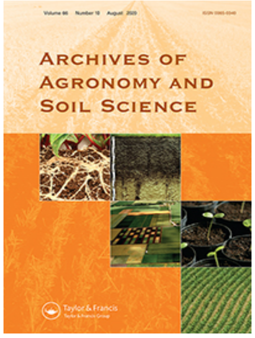

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Avocado rootstock influences scion leaf mineral content

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ABSTRACT

To test the influence of avocado rootstocks on the scion leaf ionome, the nutritional status of avocado cultivars Hass and Ettinger grafted onto 15 rootstocks was compared over 3 years. The rootstocks were of different genetic origins (West Indian or Mexican) and were clonally or reproductively propagated. The trees were grown in a high-density orchard, and were continually fertigated as is common in modern avocado orchards. Leaf mineral composition was analysed and found to be correlated with crop load. 'Hass' leaves had significantly higher levels of B, Ca, Mg, Na, P and K than 'Ettinger' leaves. Rootstocks of Mexican origin produced higher foliar Cl levels, but lower levels of Mg and Mn. Rootstocks grown from seedlings conferred higher foliar K and lower B, Ca and Mg. The results demonstrate that avocado rootstocks affect the nutritional status of the tree, by a differential mineral transport, which is indicated by the scion leaf ionome.

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Avocado; fertigation; leaf mineral content; rootstock; Hass

Introduction

Grafting is an ancient horticultural method, assumed to date back thousands of years (Melnyk and Meyerowitz 2015). It was first described in trees (Mudge et al. 2009) but today, grafting is an important method for the commercial production of vegetables and ornamentals as well (Kabiraj et al. 2017; Bergstrand 2017; Barón et al. 2019). Grafting is useful for many different applications, among them vegetative propagation, cultivar replacement, improvement of water-use efficiency, and stress resistance contribution (Mudge et al. 2009; Cantero-Navarro et al. 2016; Melnyk 2017). The relationship between the two components of a composite plant must be symbiotic or at least cooperative, as the scion is the photosynthetic part of the combination, and the rootstock supplies nutrients and water from the soil via the roots. Recent studies have shown that the scion and rootstock exchange not only nutrients and water, but also hormones, proteins and genetic macromolecules (Wang et al. 2017). There is evidence of influences in both directions – rootstock on scion and vice versa (Shu et al. 2017). To enable this close cooperation, the transport systems of the scion and rootstock must coalesce (Pina and Errea 2005). To match them properly, expertise and prior knowledge of the scion and rootstock characteristics are required (Goldschmidt 2014).

As autotrophic organisms, plants can synthesize their own organic components. This is not the case for inorganic nutrients, which must be absorbed from the environment. Nutrient assimilation is the process by which the plant incorporates minerals into vital organic substances, controlling numerous biological functions (Chietera and Chardon 2014). Some of these minerals are defined as essential elements, meaning that a deficiency or their absence will significantly impair plant growth

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Supplemental data for this article can be accessed here.

and development (White and Brown 2010). From an agricultural perspective, such deficiencies might lead to yield loss – in terms of quantity or quality – and should therefore be addressed.

The soil is the main source of minerals available to the plant (Lambers et al. 2009). Minerals pass from the roots to the foliage through the vascular system. Analysis of leaf mineral content (ionome) is a common method in agricultural practice and research to determine the general nutritional status of the plant during growth (Uçgun and Gezgin 2017), and can be used to improve yield (by adjusting fertilization levels) or to evaluate salinity damage. This method may also partially reflect the functioning of the rootstock and its reciprocity with scion (Jiménez et al. 2007; Ahmed et al. 2007; Savvas et al. 2011). When analyzing the leaf ionome, it is crucial to ensure uniformity of leaf age and physiological condition, as nutrient levels tend to change with time (Bally 2009). Other factors that may affect leaf mineral content are soil type, fruit load and leaf position (Dixon et al. 2006).

Avocado (*Persea americana* Mill.) is an important edible crop with economic significance and rapidly growing popularity among consumers (Bulagi et al. 2015; Williams et al. 2017). It is an obvious alternate-bearing species (Lovatt 2010) and this financially problematic trait has been the focus of many recent studies, using physiological and molecular approaches (Ziv et al. 2014; Lovatt et al. 2015; Salvo and Lovatt 2016; Garner and Lovatt 2016). Most commercial avocado orchards consist of grafted trees (Zafar and Sidhu 2018). The scions are of several common edible cultivars. Among them, 'Hass' is the most consumed variety (Carman et al. 2009), dominating the world industry. Common agricultural practice in avocado orchards requires planting another variety beside the major one, to serve as a pollinizer. Avocado is grown in many countries worldwide; each production area has its own climate, soil and biotic environment, and so it is crucial to choose the right rootstock, which will best support the chosen scion (Fassio et al. 2009). There are dozens of known avocado rootstocks; each of them has its own benefits and adaptations to specific conditions (Ben-Ya'acov and Michelson 1995; Whiley et al. 2007; Smith et al. 2011). There are three main genetic sources for avocado rootstocks: West Indian, Guatemalan and Mexican, which differ in their roots' absorption of minerals (Mickelbart et al. 2007). The rootstocks might originate from clonal propagation or seedlings (Ben-Ya'acov and Michelson 1995). A quantitative profile of minerals in the leaf serves as a diagnostic tool for the physiological and nutritional status of the plant (Baxter et al. 2008), which in turn critically affects growth rate and yield. Hence, the effect of a rootstock on the micro – and macronutrient status of the leaf should be considered. This effect has been studied in pear (North and Cook 2008), peach (Zarrouk et al. 2005), apple (Tagliavini et al. 1992; Fallahi et al. 2001; Cheng and Raba 2009), melon (Ruiz et al. 1997), and citrus (Zekri and Parsons 1992), among other crops.

The purpose of this study was to test the effect of rootstocks on the nutritional status of avocado trees grown under continuous fertigation management. This management practice, in contrast to the traditional system where the fertilizer was spread separately of the irrigation, exposes the roots to a relatively constant level of nutrients in the soil. We analyzed the mineral content of leaves from two commercial varieties – 'Hass' and 'Ettinger' – grafted on a wide range of rootstocks. We hypothesized that genetic origin influences the rootstock's activity as it indicates an evolutionary adaptation of the plant to its natural habitat, and that clonal rootstocks will exhibit higher uniformity in their effect, as they have the same genotype.

Materials and methods

Experimental design

In 2011, 450 avocado scions (varieties Hass and Ettinger) were grafted on 15 different rootstocks (Table S1); 12 were clonally propagated, and 3 were from seedlings. The grafted trees were planted in 2013, at Gilat Research Center, Israel (31°20′08.6″N 34°39′57.0″E). This is a semiarid Mediterranean region characterized by warm dry summers and cool winters (average annual minimum of 14.2°C and maximum 27.7°C). The average annual rainfall is 253 mm, falling mostly between November and April (Israel Meteorological Service; years 2010–2015). The soil is a sandy loam (Calcic Haploxeralf), with a pH of 8.2 and 11.5% calcium carbonate. It is composed of 50% sand, 35% silt, 15% clay, and around 0.5% organic matter (0–5 cm). The orchard was planted in five blocks, each with 15 plots. Each plot contained six trees with the same rootstock, five of them with the 'Hass' scion and one with the 'Ettinger' scion. The trees were drip-irrigated and fertigated evenly with commercial liquid fertilizer contain: 7% N, 2% P_2O_5, 7% K_2O, 300 mg kg^{-1} Fe, 150 mg kg^{-1} Mn, 75 mg kg^{-1} Zn, 11 mg kg^{-1} Cu and 8 mg kg^{-1} Mo (Shefer^{TM} +3, Fertilizers & Chemicals Ltd., Israel) twice a week, from March to October. Annual irrigation was 14,508 m^3 ha^{-1}, and annual liquid fertilization was 2940 kg ha^{-1} (of which 205.8 kg N per hectare).

Measurements

Young, fully expanded leaves were sampled (100 per plot) in October 2015, 2016 and 2017. All leaves were positioned on new-season branches, at the south side of the tree. They were washed in running distilled water and dried at 70°C in a well-ventilated oven. Each sample was ground and thoroughly mixed. Cl content was determined in leaves based on water extraction (0.1 g dry matter in 10 ml deionized water), using an MKII chloride analyzer 926 (Sherwood). N and P were analyzed using Gallery Plus (Thermo Scientific) after digesting powdered material with sulfuric acid and hydrogen peroxide (Snell and Cornelia Snell 1954). N was analyzed using Gallery Plus (Thermo Scientific). Other leaf nutrients (B, Na, Fe, P, K, Mn, Ca, Mg and Cu) were determined by digesting powdered material with nitric acid and H_2O_2 analyzed using ICP-OES 5100 (Agilent Technologies). Tree trunks were marked with solid paint above the grafting area. The circumference at this point was first measured in June 2015, and then each year after harvest at the same spot.

Statistical analysis

Statistical analyses were carried out by one-way analysis of variation (ANOVA) and multivariate analysis, with JMP 14.0 software. To compare significant differences among the various treatments, Tukey–Kramer test was used. The values were expressed as means ± standard error (SE) of the mean.

Results

We began analyzing our data as a three-factor experiment, composed by scion, rootstock and year, but there were many interactions between the research components, which made this analysis ambiguous. Therefore, the decision was to analyze each factor by itself and compare the effects from a different perspective.

Scion

Analyzing the leaf mineral content of 'Hass' and 'Ettinger' leaves, significant differences were found for 6 minerals out of the 11 tested (Table 1). 'Hass' leaves had higher levels of all 6 minerals compared to 'Ettinger'. Following this variety-related difference, the results hereafter are divided by cultivar.

Table 1. Comparison of the foliar mineral content of varieties 'Hass' and 'Ettinger'. Values are averages of 3 years (2015–2017). Underlined values are significantly different ($P < 0.05$) between varieties.

	N %	P %	K %	Cl %	Na %	B mg kg^{-1}	Ca %	Mg %	Mn mg kg^{-1}	Fe mg kg^{-1}	Cu mg kg^{-1}
'Hass'	1.417	<u>0.120</u>	<u>0.870</u>	0.167	<u>0.012</u>	<u>120.996</u>	<u>1.639</u>	<u>0.585</u>	262.554	136.876	5.654
'Ettinger'	1.430	<u>0.104</u>	<u>0.812</u>	0.162	<u>0.010</u>	<u>98.165</u>	<u>1.479</u>	<u>0.527</u>	237.630	123.738	5.472

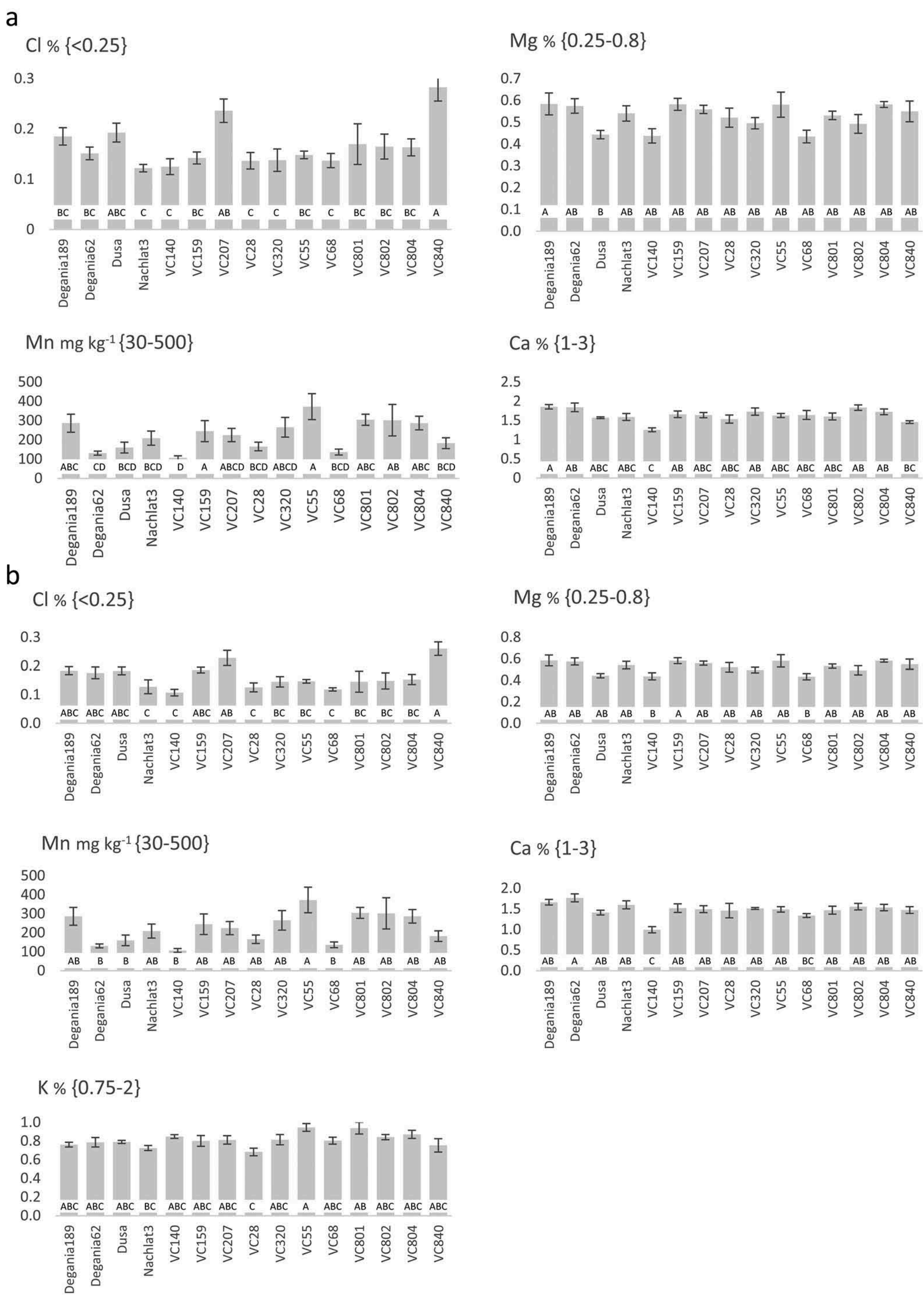

Figure 1. Effect of rootstock on the mineral level in avocado leaves. (A) 'Hass'. (B) 'Ettinger'. Minerals for which no significant effect was found are not shown here. The graphs show the averages of five replicates, each replicate is an average of 3 years' measurements. Bars represent SE. Different letters represent significant differences between rootstocks. Numbers in curly brackets next to the mineral name represent suggested ranges for avocado, following the University of California at http://ucavo.ucr.edu/General/LeafAnalysis.html.

Rootstock

Comparing the ionome of all trees, rootstocks had a significant effect on Cl, Mg, Mn and Ca levels in the leaves of both tested scions, while K level was affected by rootstock only in 'Ettinger' (Figure 1). The effect was not constant among scions. For example – the highest Mg level in 'Hass' leaves was that of 'Degania189' rootstock, and the lowest- 'Dusa'. However, in 'Ettinger' leaves the rootstock with highest Mg level was 'VC159' and the lowest- 'VC68' and 'VC140'. B, Fe, Cu, Na, N and P were not affected by the rootstocks. Among the significant minerals, Mg had the lowest difference between rootstocks (135% in 'Ettinger', 140% in 'Hass'), while Mn had the highest (350% in 'Ettinger', 326% in 'Hass').

Rootstocks also significantly affected the relative change in trunk circumference over the measurement period (Figure 2). Within 'Hass' trees, the rootstock that exhibited the highest change was VC801, while the poorest trunk growth was measured in VC320 and Nachlat3 (Figure 2). Within 'Ettinger' trees, the highest change was that of VC55 rootstock, and the lowest- of Nachlat3 and Degania 62 (Figure 2).

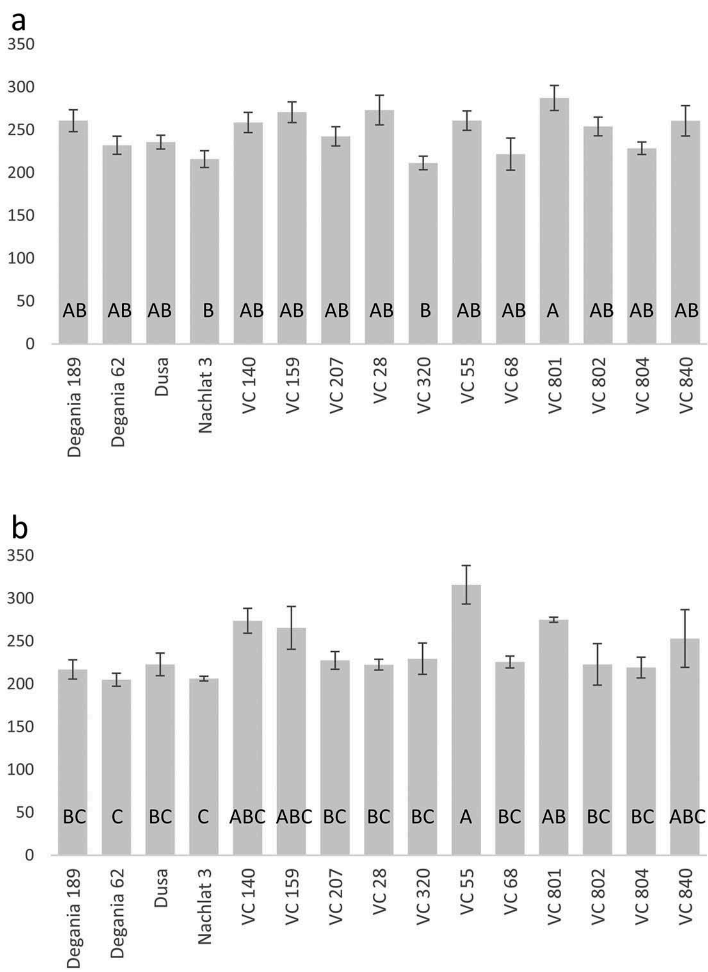

Figure 2. Effect of rootstocks on the relative change in trunk circumference of avocado trees. (A) 'Hass'. (B) 'Ettinger'. Graphs show averages of 3.5 years (June 2015–December 2017) for each rootstock. Different letters represent significant differences between rootstocks. Bars represent SE.

Significant correlations were found between trunk circumference and mineral levels in both cultivars (Figure S1). The strongest correlations (above 0.5) were with N and K in 'Ettinger' leaves.

Dividing the rootstocks according to their genetic origin, the only significant difference between the West Indian and Mexican rootstocks grafted to the 'Ettinger' scion was in the foliar Cl content. For 'Hass', Mg and Mn differed as well. In both varieties, Cl was higher with the Mexican-originated rootstocks (Table 2).

Regarding the propagation method, the varieties gave similar results: B, Ca and Mg were higher with rootstocks from seeds (Degania189, Degania62 and Naclat3, see Table S1), whereas K was higher with clonally propagated rootstocks (Table 2). No significant differences were found between propagation methods in terms of result uniformity, when comparing the coefficient of variation.

Year

When the yearly measurements were compared to the average values of 3 years, we noticed an interesting pattern: in both varieties, two similar groups were created, according to the mineral levels over the years (Figure 3). The first group, which contained Cl, B, Ca, Mg, Mn and Fe, gave low values in 2015 and 2017, and high values in 2016. For the second group, consisting of Cu, N, P and K, lowest values were in 2016, and high values in 2015 and 2017. Na showed a different pattern, with highest level in 2015 and lowest level in 2017, for both varieties.

Correlation analysis between nutrient pairs revealed two groups with opposite relations (Figure 4)- the first group contained Cl, B, Ca, Mg, Mn and Fe, and the second Cu, P, K and N. Most nutrients had

Table 2. Comparison of the foliar mineral contents in varieties 'Hass' and 'Ettinger', grafted on rootstocks of different genetic origin: West Indian (WI) and Mexican (M), or from different propagation methods: clonal vs. seed. Values are averages of 3 years (2015–2017). Underlined values are significantly different (P < 0.05) within varieties between origins or propagation methods.

	Hass		Ettinger	
	Genetic origin			
	Mexican	West Indian	Mexican	West Indian
N (%)	1.46±0.07	1.41±0.11	1.47±0.12	1.43±0.12
P (%)	0.12±0.01	0.12±0.02	0.10±0.01	0.11±0.01
K (%)	0.87±0.08	0.88±0.12	0.78±0.10	0.82±0.11
Cl (%)	**0.24±0.06**	0.15±0.04	**0.22±0.05**	0.15±0.04
Na (%)	0.011±0.005	0.012±0.005	0.011±0.004	0.011±0.002
B (mg kg^{-1})	114.75±19.08	121.52±19.31	89.35±16.43	97.33±19.42
Ca (%)	1.55±0.12	1.65±0.24	1.45±0.16	1.49±0.25
Mg (%)	0.54±0.06	**0.6±0.090**	0.51±0.08	0.53±0.09
Mn (mg kg^{-1})	190.57±69.16	**274.11±129.47**	192.27±69.51	230.45±116.67
Fe (mg kg^{-1})	127.57±23.39	136.86±41.15	117.72±22.88	124.17±41.00
Cu (mg kg^{-1})	5.96±0.62	5.63±0.69	5.63±0.84	5.41±0.83

	Hass		Ettinger	
	Propagation method			
	Clonal	Seed	Clonal	Seed
N (%)	1.43±0.11	1.39±0.08	1.46±0.11	1.39±0.14
P (%)	0.12±0.02	0.12±0.01	0.1±0.010	0.1±0.010
K (%)	**0.89±0.11**	0.83±0.10	**0.82±0.11**	0.76±0.08
Cl (%)	0.16±0.06	0.16±0.04	0.16±0.06	0.16±0.05
Na (%)	0.012±0.005	0.013±0.004	0.011±0.003	0.011±0.002
B (mg kg^{-1})	118.01±17.67	**128.54±22.87**	93.26±16.36	**105.64±25.41**
Ca (%)	1.59±0.21	**1.78±0.22**	1.43±0.22	**1.68±0.19**
Mg (%)	0.58±0.08	**0.63±0.09**	0.52±0.09	**0.57±0.08**
Mn (mg kg^{-1})	270.02±127.81	225.57±111.53	226.89±113.45	208.75±97.12
Fe (mg kg^{-1})	137.95±42.95	126.13±15.81	120.73±31.08	131.43±58.86
Cu (mg kg^{-1})	5.75±0.69	5.46±0.65	5.49±0.82	5.27±0.91

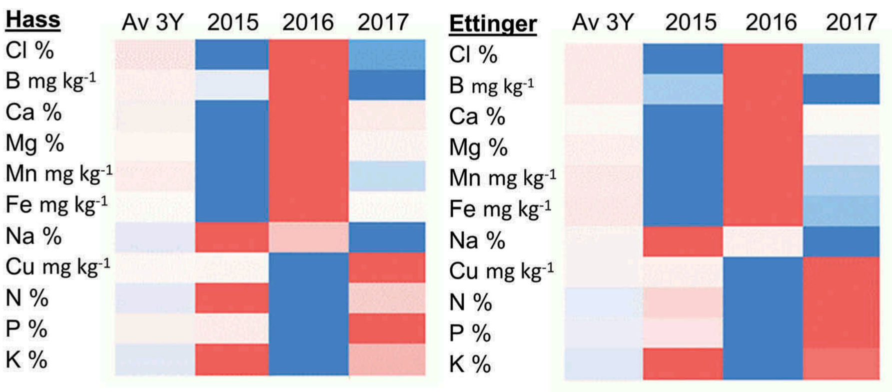

Figure 3. Yearly alternating patterns in mineral content of 'Hass' and 'Ettinger' leaves. Each year's average, from all rootstocks, was compared to the average of 3 years (Av 3Y). Higher than average values are shaded red, and lower than average in blue.

significant correlations with the others. In 'Hass' leaves, Na had a significant correlation only with Fe and Cu, while in 'Ettinger' it had a significant correlation with Cu, Ca, B and N. The strongest correlations (more than 0.7) within the 'Hass' leaves were between Mg and Ca, P and Cu, Mg and Mn, N and P, and Mg and N (Figure 4A). Within the 'Ettinger', the strongest correlations were between B and N, Mg and Ca, Mg and Mn, Cu and N, Cu and P, and N and P (Figure 4B).

Discussion

Fertigation management is expanding to many orchard crops, as an effective and simple method of applying a desired fertilizer through the irrigation water (Mmolawa and Or 2000). Fertigation enables a stable and constant habitat in the root zone, thereby minimizing the effect of environmental and technical factors on mineral absorption by the plant (Bar-Yosef 1999). These properties make it an ideal strategy to study root function. Rootstocks supply nutrition to their scions and their function is of great value to the plant. In this study, we found that under fertigation management, avocado rootstocks affect the mineral content of the scion's leaves.

The nutrients that were most affected by the rootstock were Cl, Mg, Mn and Ca, and in 'Ettinger' trees, also K. Mg, Mn and Ca levels are indicators of leaf age, as they tend to accumulate during vegetative growth (Koo and Young 1977; Nachtigall and Dechen 2006). Their internal correlations in our 3-year results were high and significant, supporting a similar accumulation pattern. In apple trees, Ca and Mn continue to accumulate in the leaves even after shoot growth has stopped, and Mg level increases gradually until fruit harvest (Cheng and Raba 2009). As all leaves were diagnostic, the same age and position, we can assume that the discrepancy reported here in these nutrients' levels reflects the rootstock's influence on vegetative growth. To check this assumption, the relative change in trunk circumference was examined. Significant differences were found between the rootstocks' effects on trunk circumference in both 'Hass' and 'Ettinger'. The lowest relative change for both varieties was in the trunk circumference of 'Nachlat 3' rootstock, which is of a reproductive propagation method. The rootstocks that had the greatest vegetative growth were of clonal propagation- 'VC 801' in 'Hass', and 'VC 55' in 'Ettinger'. However, the correlations between vegetative growth and foliar nutrient levels were low although significant. An in-depth evaluation of the rootstocks performance strengthened the significant influence of their propagation method and genetic background on the scion nutritional status. This is in line with previous works, in which avocado leaves growing on rootstocks of different races exhibited different nutrient levels. For example, leaves of avocado trees grafted on Mexican rootstocks had higher N content than those grafted on Guatemalan rootstocks, but lower Mg and Ca contents (Mickelbart

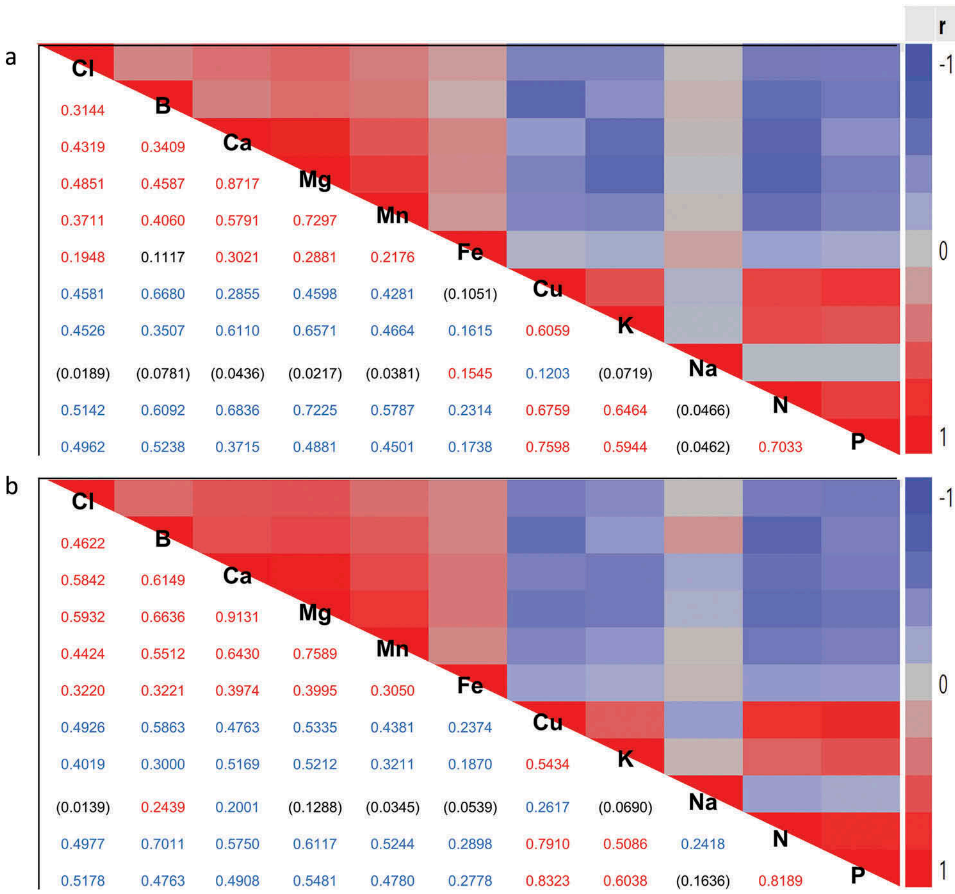

Figure 4. Multivariate clustering of correlations between nutrients in avocado leaves. A: 'Hass', B: 'Ettinger'. Data are based on 3-year averages of the nutrients in all rootstocks. Non-significant values are in parentheses. Blue shading – negative correlations; red shading – positive correlations.

et al. 2007). Similar results were observed when Mexican rootstocks were compared to West Indian ones – higher N and K, lower Ca and Mg (Willingham et al. 2006). In general, Cl content was highest in leaves of Mexican rootstocks (Lahav and Aycicegi-Lowengart 2003). Our results provide the basis for further research into genetics-associated nutritional mechanisms in rootstocks.

Though the rootstocks significantly affected leaf mineral composition, this organ belongs to the scion, and the cultivar has its own influence over it. Comparisons of leaf nutrients in 'Hass' and 'Ettinger' trees have revealed a consistently higher level of some of the nutrients tested in 'Hass' (Lahav and Kadman 1980; Kurtz et al. 1992), in line with our results. However, the greatest difference between varieties was of 19% in B levels, while the rootstocks had effects of more than 300% regarding Mn levels.

Avocado is an alternate-bearing crop (Garner and Lovatt 2008), making it an interesting system to compare the productivity-related nutritional status of the plant under constant conditions. In our orchard, 2015 and 2017 were 'off' years, and 2016 was an 'on' year, differing in 40-50% in yield (unpublished data). We found that the leaf minerals could be sorted into two groups in terms of their distinct response to crop load, which were identical to the groups created by correlation analysis. The first group contains Cl, B, Ca, Mg, Mn and Fe, whose levels were positively correlated with yield. The second group – N, P, K and Cu – showed the opposite pattern: high levels when crop yield was low and vice versa. The inverse correlation between leaf NPK contents and yield is known, stemming from the strong fruit sink (Awasthi and Kaith 1989; Choi et al. 2010; Muhammad et al. 2015). The high levels of Cl and Ca in the leaves of an 'on' year might be explained by the fact that heavy fruiting increases the tree's transpiration rate (Silber et al. 2013), and these elements move through the plant with the water flow (Kirkby and Pilbeam 1984; White and Broadley 2001). Our results underscore the effect of crop load on plant nutritional status, which must be considered when analyzing leaf composition.

In conclusion, fertigation provides a reliable and convenient environment for rootstock testing. Avocado rootstocks influence the leaf ionome, in correlation with crop load, as well as with the propagation method and genetic source of the rootstocks. These data need to be taken into consideration when interpreting diagnostic leaf mineral levels into a fertilization program.

Disclosure statement

No potential conflict of interest was reported by the authors.

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