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The role of rootstock and its genetic background in plant mineral status: the relationship between petiole analyses and deficiency symptoms

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ABSTRACT

Rootstocks are an important means of adapting grapevine to environmental conditions whilst conserving the typical features of scion genotypes. Rootstocks not only provide tolerance to Phylloxera, but also ensure the supply of water and mineral nutrients to the scion. We take advantage of the large diversity of rootstocks used worldwide to facilitate this adaptation. The aim of this study was to characterise rootstock regulation of scion mineral status and its relationship with scion development.

Vitis vinifera cvs. Cabernet-Sauvignon, Pinot noir, Syrah and Ugni blanc were grafted onto 55 different rootstock genotypes and planted as three replicates of five plants in sandy gravelly soil near Bordeaux, France. In 2020 and 2021, petiolar concentrations of 13 mineral elements (N, P, K, S, Mg, Ca, Na, B, Zn, Mn, Fe, Cu and Al) were measured at veraison. Winter pruning weight, shoot vigour, leaf chlorophyll content, bud fertility and yield were measured. Magnesium deficiency severity was visually scored for each plant. Rootstocks were grouped according to their *Vitis* parentage background when at least 50 % of a *Vitis* species was present in order to determine whether the petiole mineral composition could be related to the rootstock genetic parentage.

Scion, rootstock, and their interactions had a significant influence on petiole mineral content and explained the same proportion of phenotypic variance for most mineral elements. Rootstock effect explained 9, 28 and 45 % of the mineral content variance for N, Mg and S respectively. This unique experimental design showed that the rootstock effect was higher than the scion effect on the petiole concentration of a large majority of mineral elements. The genetic background *V. riparia* increased the probability of low petiolar P and Mg contents. The severity of Mg deficiency symptoms varied depending on the rootstock. The differences in mineral status conferred by rootstocks were not significantly correlated with vigour or fertility.

The evaluation of Mg levels by petiole analysis and the intensity of deficiency symptoms showed for the first time the variability of the thresholds of satisfactory mineral nutrition between rootstocks. Therefore, fertiliser management should take the rootstock variety into account.

KEYWORDS: *Vitis*, grapevine, plant material, mineral deficiency, rootstock × scion interaction, magnesium

INTRODUCTION

Since the late 19th century, grapevine has been grown grafted in most of the world largely because of Phylloxera (*Daktulosphaira vitifoliae*). Rootstocks allow tolerance to phylloxera, but they also play a major role in water and mineral nutrient absorption, as reviewed by Ollat *et al.* (2016). They strongly interact with scion genotypes and modify whole plant development through the modification of yield and vigour in an environmentally dependent manner (Tandonnet *et al.*, 2010; Tandonnet *et al.*, 2008; Tardáguila *et al.*, 1995). Differences in rootstock behaviour have a strong influence on grape growers' choice for soil adaptation, yield, fertiliser requirements and canopy management (Ibacache *et al.*, 2020). Rootstocks play an important role in adaptation to environmental conditions when aiming to conserve the typical features of the currently used scion genotypes.

Plants absorb elements from the soil and atmosphere and incorporate them into their tissues. Mineral elements can be classified in two categories: macroelements and microelements (Maathuis, 2009). Macroelements, such as nitrogen (N), phosphorus (P), potassium (K), magnesium (Mg), sulphur (S) and calcium (Ca), represent the major requirements of plants in terms of quantity. They are required for structural roles, as well as energy metabolism, protein and nucleic acid synthesis, osmotic adjustment, ion homeostasis and signalling. By contrast, microelements, such as boron (B), zinc (Zn), manganese (Mn), iron (Fe), copper (Cu) and aluminium (Al), are essential for plant development, but are required in low quantities as catalytic elements involved in metabolic reactions, such as enzymes or cofactors (Marschner, 2012).

Mineral deficiencies and toxicities exist in viticulture and they can have a strong negative impact on vegetative development, fruit development and yield (Bavaresco *et al.*, 2010). Deficiencies can be due to the lack of a mineral or induced by other parameters, such as an excess of a competitive mineral, an inappropriate soil pH or the presence of active limestone for iron. Most of the time, symptoms of deficiency can be visually observed on leaves (Marschner, 2012), but they can be also be observed at whole plant level and with yield-related traits at different seasonal timings, such as early season, blooming, fruit set and veraison (Delas, 2011). When determining plant mineral status, petiole nutrient analysis is a reliable indicator (Schaller, 2008).

Grafting grapevine impacts the mineral content of the different compartments of the plant, such as the shoots, roots, leaves, berries and petioles (Carles *et al.*, 1966; Dalbó *et al.*, 2011; Delas and Pouget, 1979; Pachnowska and Ochmian, 2018). Rootstocks also react differently to fertiliser management, as the response of petiole and leaf mineral content to fertiliser application depends on the rootstock (Delas and Pouget, 1979) and soil characteristics (Fisarakis *et al.*, 2005). In addition, scions differ in tissue mineral content, but few studies have included the analysis of several scions and rootstocks. When different scions and rootstocks are both studied, statistically they are often independently analysed (Dalbó *et al.*, 2011; Ibacache and Sierra, 2009; Kocsis and Lehoczky, 2000; Wolpert *et al.*, 2005). In some cases, the two factors are statistically studied together, but without the assessment of the relative importance of the scion and rootstock factors (Wooldridge *et al.*, 2010). The differences in mineral petiole concentrations induced by the rootstock parentage has rarely been studied; Wolpert *et al.* (2005) studied the effects of genetic backgrounds on petiole K concentrations, and Gautier *et al.* (2020) studied the effects of the genetic background on petiole P concentrations. In both these studies, a descriptive approach was used and these studies were based on less than 15 rootstock genotypes.

The first written reference to the impacts of rootstock on foliar deficiency symptoms was done by Bovay and Gallay (1956). Since then, rootstocks have been classified according to their ability to satisfy scion mineral requirements, but this has only been based on petiole mineral content (Cordeau, 1998; Ibacache and Sierra, 2009). The relationship between petiole analyses and deficiency symptoms observed in the field has never been determined. Magnesium deficiency symptoms have been used to describe the behaviour of various scions (Pedò *et al.*, 2019) and rootstocks linked to the percentage of bunch stem necrosis (Spring *et al.*, 2012), but without comparison with tissue mineral analyses (Provost *et al.*, 2021).

The aims of this study were 1) to evaluate the relative effects of the scion and the rootstock on scion petiolar mineral content, using a very wide selection of rootstocks and four scions, 2) to determine whether the scion mineral content is related to the rootstock genetic backgrounds, 3) to characterise the relationship between petiole concentrations and mineral deficiency symptoms by suggesting a new classification of rootstocks, and 4) to study the influence of the Mg deficiency on growth-related traits.

MATERIALS AND METHODS

1. Plant material

The studied plant material is part of the experimental design GreffAdapt (Marguerit *et al.*, 2019). *Vitis vinifera* cvs. Cabernet-Sauvignon clone 169, Pinot noir clone 113, Syrah clone 524 and Ugni blanc clone 481 were grafted onto 55 different rootstock genotypes. Thirty rootstocks commercially used in France and 25 rootstocks used in other countries were selected for relevant characteristics with respect to lime-induced iron deficiency chlorosis, drought and conferred vigour traits. The complete rootstock list can be found in Table 1.

The rootstocks were grouped according to their parentage to reduce the number of treatment groups. The parentage was assigned when at least 50 % of a genetic background was present (Maul *et al.*, 2023; Riaz *et al.*, 2019). If a parent was not known, the theoretical genetic background concerned was deleted. Some rootstocks (Nemadex AB, Georgikon 121, Georgikon 251, 1616C, Freedom, Dog Ridge, Harmony, and Ramsey) were removed from this

TABLE 1. Rootstocks classified according to their dominant parentage for the genetic background study, the number of rootstocks per genetic background and the number of plants studied for each year.

Genetic backgrounds	Rootstocks	Number of rootstocks	Number of plants in 2020	Number of plants in 2021
V. riparia	Riparia Gloire de Montpellier, 106-8MGt, 125-1MGt, 196-17Cl, 44-53M, Börner, Gravesac, Vialla	8	183	184
V. riparia × *V. rupestris*	101-14MGt, 4010C, Schwarzmann, 3309C	4	96	96
V. rupestris	Rupestris du Lot, 216-3Cl	2	46	48
V. berlandieri × *V. rupestris*	1045P, 1103P, 110R, 140Ru, 1447P, 57R, 775P, 779P, 99R, V15	10	226	224
V. berlandieri × *V. riparia*	125AA, 157-11C, 225 Ru, 34EM, 420A, 5BB, Binova, M3, RSB1, SO4, Téléki5C, 161-49C, Téléki8B	13	292	286
V. berlandieri	150-15M, Evex 13-3, Evex 13-5, Fercal, M1, M4	6	109	102
V. berlandieri × *V. vinifera*	333EM, BC2, 41B, Georgikon 28	4	93	92

part of the study, because they have complex parentages and to avoid a single genotype being used to represent a parentage category. Moreover, the genetic background *V.×champinii* was not studied, because it is already a cross between *V. candicans* and *V. rupestris Scheele*. *V.×champinii* was also poorly represented in our dataset. A final panel of seven parentages was thus formed with 47 rootstocks composed of *V. berlandieri, V. berlandieri × V. riparia, V. berlandieri × V. rupestris, V. berlandieri × V. vinifera, V. riparia, V. riparia × V. rupestris and V. rupestris* (Table 1) to study the effect of genetic background on the scion.

2. Experimental design

The experimental vineyard GreffAdapt is located on the "Domaine de la Grande Ferrade" near Bordeaux, France (44°47'26.7"N 0°34'26.5" W). It has an area of 0.8 ha and was planted in 2015 in three blocks of five vines each on sandy gravelly soil. The Bordeaux area has an oceanic-type climate which is characterised by very mild winters and warm summers. In the two years of the study, 2020 was warmer than 2021, with an average growth period temperature of 19.6 °C versus 18.2 °C respectively. The 2021 vintage was characterised by a very wet May to June period with a total of 290 mm of rainfall over these two months (Supplementary Table 1). The soil resistivity and pedological characteristics were studied to assign the block positions before plantation and the genotypes were completely randomised inside each block. Each rootstock × scion combination comprised five replicates in each block so that there was a total of 15 replicates in the trial. The first and last rows of the trial were buffer vines, as were the first and last 3 plants of each row to avoid a border effect; no data was collected from these vines.

The plantation density of the vineyard was 6250 vines/ha with a row spacing of 1.6 × 1 m. During the experiment in 2020 and 2021, the vines were 5 and 6 years old respectively. The experimental plot had never been previously fertilised; however, there is a disequilibrium in the soil Mg and K ratio (K/Mg >> 1), resulting in induced Mg deficiency through an excess of K. In this vineyard, the first organo-mineral horizon (0-35 cm) is composed of about 2 % of organic matter. The cation exchange capacity (CEC) of the soil is low (< 7 $cmol^{+}/kg$), emphasising the deficiency in Mg, and the pH is within the classic range of between 6 and 7 (Supplementary Table 2).

During winter, each vine was pruned: one cane with six buds and one spur with two buds were kept; i.e., eight latent buds for Guyot mixte training. Pruning severity varied by one to two buds depending on plant vigour.

During the vegetative period, a spontaneous cover crop was left to grow between each row and mowed when required. Therefore, the ground between the rows was not tilled, but the ground under the vines was mechanically tilled. In terms of canopy management, all the shoots were positioned within catch wires on a vertical trellis.

3. Phenotyping measurements

3.1. Petiole sampling and analysis

In 2020 and 2021, a sample of eight petioles was collected on six replicates; i.e., on two vines per blocks per rootstock × scion combination at mid-veraison (Supplementary Table 3). The second and fourth plants were sampled, so that the neighbouring rootstock was the same as the plant studied. Petioles were harvested in the cluster zone between the fourth and the sixth node and dried in an oven at 60 °C. Petioles were collected from shoots emerging from the cane to reduce any possible source of heterogeneity between the cane and the spur sides. Phenology and phytomer modify leaf mineral content (Harris *et al.*, 2021), so care needs to be taken when collecting the leaves of the same phenology and phytomer. Petiolar concentrations of 13 mineral elements were quantified by Waypoint Analytical Virginia (Richmond, VA, USA), which included the macronutrients N, P, K, S, Mg, Ca, Na, and the micronutrients B, Zn, Mn, Fe, Cu, and Al. Mineral element concentrations were determined by an inductively coupled plasma mass spectrometer (ICP-OES MS 730-ES) except for N concentration, which was determined by a Leco FP-528 instrument, an N determinator. Concentrations are expressed in terms of percentage of dry weight (w/w) for macroelements and parts per million (ppm) for microelements. A standard control sample was added to at least twelve replicates each year to check the stability of the analysis between the different scions over the two years (Supplementary Figure 1).

3.2. Grapevine growth

The annual growth of each grapevine was evaluated by winter cane pruning weight. The number of shoots of each vine was counted and vigour was calculated by dividing the winter cane pruning weight by the number of shoots. Measurements were performed on each single plant; i.e., 15 replicates annually for each rootstock × scion combination.

3.3. Yield

In this trial, no yield regulation was carried out. At harvest, the number of bunches per grapevine was counted and the bunch weight of each grapevine of the vineyard measured. The fertility of each plant was calculated as the ratio between the number of clusters and the number of shoots.

3.4. Dualex measurements

Estimations of chlorophyll, anthocyanin and flavonol contents, and nitrogen balance index (NBI) in vine leaves were measured using the hand-held fluorescence-based sensor Dualex (Force-A) (Goulas *et al.*, 2004). The NBI is related to the N status of the grapevine and proportional to the chlorophyll/flavonol ratio. Measurements were done at mid-veraison on three different leaves per plant and three plants per block for each combination of rootstock × scion × block combination; i.e., 3 × 3 × 3 values. Data on the first mature leaves from the apex of primary shoots were assessed.

3.5. Mineral deficiency observations

In 2021, visual signs of Mg deficiency in each plant were scored. The observations were qualitative and scores between 0 and 3 were assigned: 0 = no signs of Mg deficiency symptoms, 1 = lower leaves expressed Mg deficiency, 2 = at least the bottom half of the canopy expressed Mg deficiency, and 3 = all leaves expressed Mg deficiency (Figure 1).

4. Statistical analyses

All statistical analyses were performed using R v.4.2.0 Statistics Environment (R Core Team., 2014) and the ‘stats’, ‘agricolae’ ‘nlme’ and ‘corrplot’ packages with RStudio.

FIGURE 1. Magnesium deficiency rating scale: 0 = no Mg deficiency observed, 1 = lower leaves expressed Mg deficiency, 2 = at least the bottom half of the canopy expressed Mg deficiency, and 3 = all leaves expressed Mg deficiency symptoms.

4.1. Performing ANOVA to estimate the relative effects of scion and rootstock on mineral content variability

A three-way analysis of variance with interaction effect (ANOVA) was performed on all 55 rootstocks to characterise the importance of the different factors (scion, rootstock and block). This test was performed to partition out the contribution of different factors to the variation in a continuous variable via the sums of squares. The effect of each factor on each petiolar nutrient concentration was determined by the percentage of variance explained (PVE) by this factor. In an analysis of variance, the PVE is the ratio of the sum of squares between groups divided by the total sum of squares. The ANOVA assumptions were checked: the normality of the model residuals distribution was checked using a Q-Q plot and the homogeneity of the variances using a ‘residuals versus fits’ plot. Each year was analysed independently, because the experiment and values were not independent: the samples were collected from the same plants in different years.

4.2. Two-way contingency tables and chi-square tests to study the dependence between mineral status and genetic background

To study the effects of the genetic backgrounds of 47 rootstocks, the mineral content values for N, P, K and

Mg were grouped according to status: excess, optimum and deficiency based on the thresholds of Delas (2011) (Supplementary Table 4). Not all elements were studied, because not all thresholds are known in viticulture, and some deficiencies are never observed in the vineyard. B and Zn were not studied, because there was little variability in terms of plant mineral status for these elements, which all had optimum status. Contingency tables for each mineral element were established based on genetic background and mineral status. The dependence between the genetic background and the mineral status was determined by applying a chi-square test (significance level p-value < 0.05) to the contingency tables. A chi-square test of frequency was performed when a total of individuals greater than 30 and no theoretical number less than 5 were respected (Agresti, 2019).

To understand the relationship between genetic background and mineral status, we studied standardised residuals for each genetic background and mineral status that followed a standard normal distribution. From the sign of the standardised residuals (i.e., + or -), we were able to determine whether a genetic background group induced more or fewer plants in a mineral status group for a given element. The sign of the standardised residuals measures whether the difference between the obtained values and the theoretical values in a category (when the qualitative variables are truly independent) is higher (sign +) or lower (sign -) (Agresti, 2019). To determine the significance of the relationship, the error rate, alpha, was set at 0.05 (*), 0.01 (**) or 0.001 (***), which respectively translates into z-critical values |1.96|, |2.58| and |3.09|.

4.3 Pearson correlations to understand the relationship between mineral content, and growth- and yield-related traits

The relationships between growth- and yield-related traits and mineral contents were studied by Pearson correlations plotted in a correlation matrix. The values were averaged by scion/rootstock combination. Only relationships with a Pearson coefficient correlation superior to 0.4 and a p-value below 5 % appear on the correlation matrix.

RESULTS

1. The rootstock effect was stable in both years and generally stronger than other factors

ANOVA models were used to study the block, scion and rootstock factors, and all the interactions between these factors (Figure 2). The three main factors had a highly significant effect (p-value < 0.001) for each mineral, except for the block effect on N in 2021. The double and triple interactions were mostly significant except for elements with a white cell (Figure 2). The two dominant factors were the rootstock and the scion, the number of minerals that had a PVE by these factors of over 15 % being 10 and 5 out of 12 respectively. The range of the PVE by rootstock was 7.4 % for N to 44.7 % for S and the range of the PVE by scion was 1.6 % for P to 24.1 % for K over the two years. For P, K, S, Mg, and Ca the rootstock effect was equivalent to the scion effect and sometimes even higher.

Elements	Block	Rootstock	Scion	Rootstock × Scion	Block × Rootstock	Block × Scion	Block × Rootstock × Scion
2020							
N	5.4	7.4	21.1	16.2	12.4	0.9	25.8
P	6.6	16	1.6	20	11.4	1.4	23.7
K	0.8	16.8	20.6	11.9	9.9		24.4
S	0.9	25	24.1	11.3	7.3	0.8	16.3
Mg	3.7	21.4	3.1	14.4	15.3	0.7	23.8
Ca	3.8	15.4	10.1	18.1	9.7	2.1	27.8
2021							
N		9.3	4.4	13.5	11.8	3.1	27
P	0.5	18	8.3	16.9	12.3		21.9
K	8.6	20.6	23.3	12.3	8.3	0.8	16.6
S	4.6	44.7	4.2	10.8	8.4	1.3	14.3
Mg	5.1	27.5	11.2	14.7	10.4		19.3
Ca	4.3	16.6	20.3	15.3	7.9	0.9	22.5

PVE (%)
ns
<5
5-10
10-15
15-20
>20

FIGURE 2. Percentages of variance explained (PVE) by the factors block, rootstock and scion and their interactions obtained by ANOVA-test of petiole macroelements concentrations in 2020 and 2021.

*White cells = not significant (p-value > 0.05), coloured cells = highly significant (p-value < 0.001).

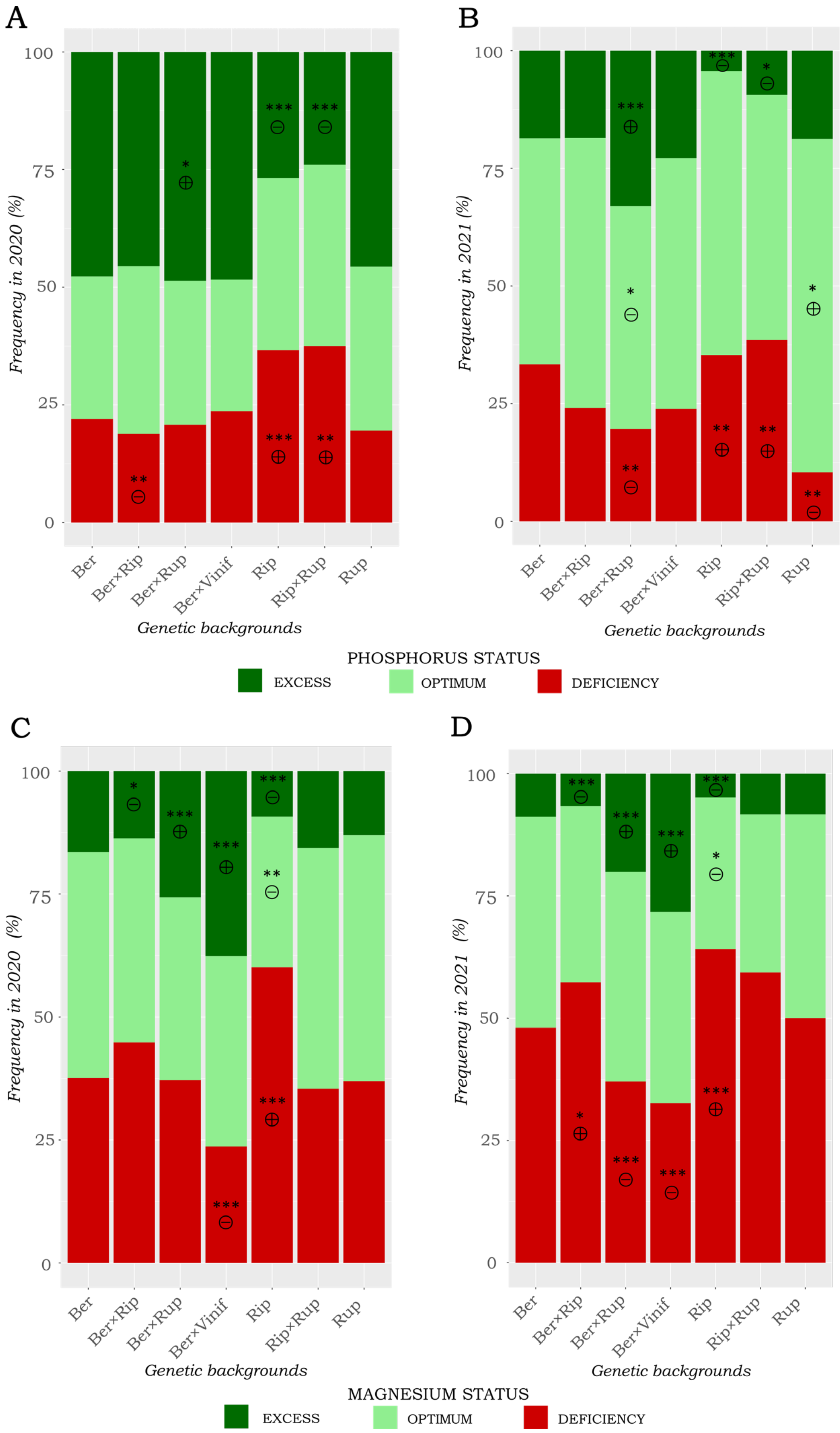

FIGURE 3. Distribution of P (A, B) and Mg (C, D) status according to rootstock genetic background in 2020 (A, C) and 2021 (B, D).

*Asterisks indicate statistically significant effect of rootstock genetic background. *, ** and *** represent statistical differences p-value ≤ 0.05, 0.01 and 0.001 respectively. The sign of standardised residuals (+ or -) shows whether a genetic background increased or decreased the proportion of plants in a given category.

For example, for Mg, the PVE by scion was 3 % (2020) and 11 % (2021), while the PVE by rootstock was 21 % (2020) and 28 % (2021). The strongest interaction occurred for block × rootstock × scion, with a range of between 14.3 and 27.8 %, and the second strongest was rootstock × scion, with a range of between 10.8 and 20 %. The block × scion interaction seemed to be negligible in this study. For P and Mg, the dominant factor was the rootstock, and other factors had only slight effects compared to the rootstock in the two-year study. The rootstock effect was also stable from the first year to the next. The average of differences in absolute PVE between 2020 and 2021 for each macroelement was 6 for rootstock effect, while it was 11 for the scion effect.

TABLE 2. P-values of chi-square tests of the independence between rootstock genetic background on macroelement status in 2020 and 2021 (without *V.* × *champinii* genetic background).

	P-value	
	2020	2021
N	0.01**	0.63
P	1.8x10-06***	6.8x10-12***
K	0.43	3.5x10-03***
Mg	9.0x10-11***	2.1x10-12***
Ca	1.0x10-05***	4.5x10-04***

*Asterisks indicate a statistically significant dependency of the mineral status on genetic background. *, ** and *** represent significant statistical effect at P ≤ 0.05, 0.01 and 0.001 respectively.

2. Genetic backgrounds influence the mineral status of most macroelements

The genetic background of the rootstock showed a significant effect on the scion N, P, K, Mg and Ca status (p-value < 0.05). For these mineral elements, the genetic background significantly influenced the proportion of plants that were in deficiency, optimum or excess for at least one year (Table 2). Of the elements studied, we focused on P and Mg status, because they were significantly dependent on the genetic background over the two years of the study and had the strongest effect.

In 2020 and 2021, three genetic backgrounds modified P status across the two years (Figure 3.A and B): *V. riparia* and *V. riparia* × *rupestris* rootstocks increased P deficiency and reduced P excess, whereas *V. berlandieri* × *V. rupestris* rootstocks increased P excess. In addition, in 2020, *V. berlandieri* × *V. riparia* reduced P deficiency and in 2021 *V. rupestris* and *V. berlandieri* × *V. rupestris* also reduced P deficiency and increased the frequency of scions with optimum P status.

In 2020 and 2021, four genetics backgrounds modified Mg status. The same genetic backgrounds were affected during the two years (Figure 3.C and D); *V. berlandieri* × *V. riparia, V. berlandieri* × *V. rupestris, V. berlandieri* × *V. vinifera,* and *V. riparia.* Seven out of nine significant rootstock genetic background effects on Mg status were common to both years: rootstocks with a *V. berlandieri* × *V. riparia* genetic background had fewer plants with Mg-excess; rootstocks with a *V. berlandieri* × *V. rupestris* genetic background had more plants with Mg-excess; rootstocks with a *V. berlandieri* × *V. vinifera* genetic background had fewer Mg-deficient plants and more Mg-excess plants; and finally, rootstocks with a *V. riparia* genetic background had less plants with Mg-excess and Mg-optimum, but more plants with Mg-deficiency.

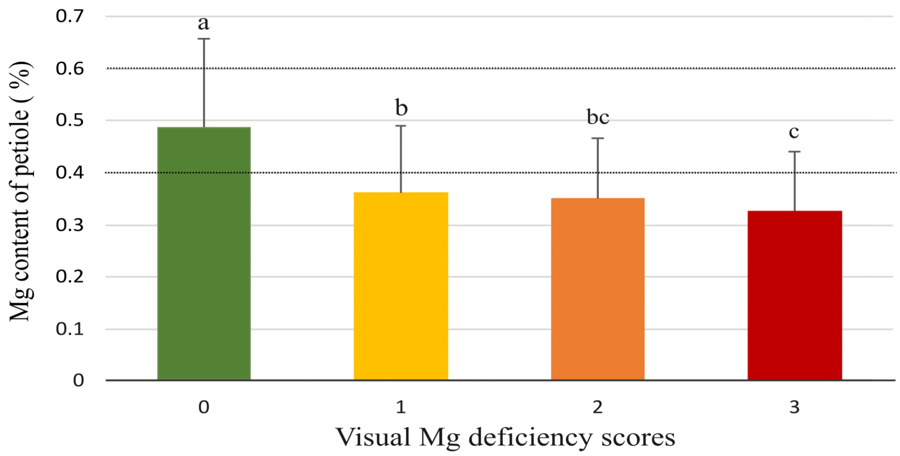

FIGURE 4. Average petiole Mg content at veraison in relation to visual Mg deficiency symptoms scores.

*Significant effect of Mg deficiency symptoms scores was tested by an ANOVA-test (p-value < 10-16). Error bars represent the standard deviations, and letters represent statistical groups obtained by a Student-Newman-Keuls test. Space between dotted lines represents the optimum of Mg-content as defined by Delas (2011).

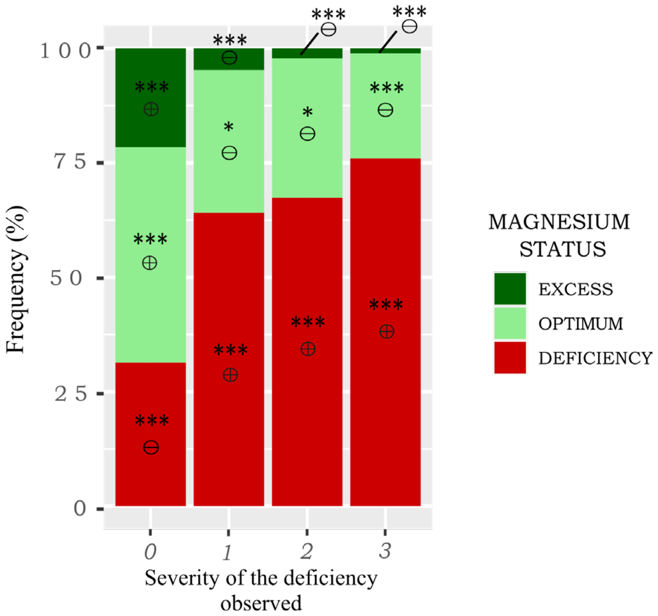

FIGURE 5. Distribution of Mg status based on petiole mineral analysis in relation to visual Mg deficiency symptom scores.

*Asterisks indicate statistically significant effect of Mg deficiency symptom intensities. *, ** and *** represent statistical differences p-value ≤ 0.05, 0.01 and 0.001 respectively. The sign of standardised residuals (+ or -) shows whether the severity of the deficiency increased or decreased the proportion of plants in a given category.

In 2021, genetic background affected K content in only a few cases. Rootstock with *V. berlandieri* and *V. berlandieri* × *V. vinifera* and *V. rupestris* backgrounds had more plants with K deficiency and less plants with K excess. By contrast, the rootstocks with *V. riparia* genetic background induced the highest proportion of plants with K-excess and the lowest with K-deficiency (Supplementary Figure 2).

3. From a relationship between petiole content and plant functioning to a mineral nutrient classification of the rootstocks

The higher the visual Mg deficiency score, the lower the Mg content in the petiole (Figure 4). The mean value for the non-visual Mg deficiency symptoms treatment group (score of 0) was above 0.4 %, while the petiolar Mg content of the plants showing Mg deficiency symptoms (scores of 1 to 3) was below 0.4 % (Figure 4). However, there is considerable variability in the relationship between Mg deficiency symptoms and petiole Mg content, as indicated by the high standard deviations shown in Figure 4.

The distribution of mineral status based on mineral analysis for each Mg deficiency score is shown in Figure 5. The mineral analysis showed that 30 % of the plants that did not show Mg deficiency symptoms were found to be Mg deficient based on their petiole content. Similarly, approximately 30 % of the plants in the deficient categories (1-3) had optimum or excess Mg status.

The rootstock effects on scion Mg deficiency symptoms and petiolar Mg concentrations were highly variable (Figure 6). In most cases (43/55 rootstocks), Mg deficiency symptoms were consistent with petiole Mg concentrations. For example, rootstocks such as M3 and Georgikon 121 induced few visual Mg deficiency symptoms in the scion and high proportions of plants with optimum or excess petiole Mg concentrations. Similarly, rootstocks such as 1616C and 44-53M induced a high proportion of plants with high visual Mg deficiency symptoms and low petiolar Mg concentrations. However, 12 out of 55 rootstocks showed some inconsistency between the visual Mg deficiency symptoms and petiole Mg concentrations. For example, 87 % of plants grafted onto Téléki8B showed no visual Mg deficiency symptoms, but 50 % had deficit Mg status based on petiole analysis; by contrast, 80 % of plants grafted onto 196-17Cl showed visual Mg deficiency symptoms, but the petiole analysis revealed 45 % to an optimum and excess Mg status.

4. There were few relationships between growth and yield-related traits, and all petiole mineral contents

A typical positive correlation between winter pruning weight and vigour was found in both years of the study (Figure 7). Furthermore, a strong significant positive correlation was observed between petiole K and B concentrations in both 2020 and 2021 (Figure 7). However, no other robust correlations between mineral elements were found between growth and yield-related traits and mineral composition over both the years of study (Figure 7). In 2021, petiole Mg contents were related to Mg deficiency symptoms, but showed no significant correlation with other traits (Figure 7.B). However, growth and yield-related traits varied between grapevines with different Mg deficiency scores, for example, between scores 0 and 3, vigour varied by 10 g/shoot and the number of bunches per plant by 0.6.

FIGURE 6. Rootstock classification based on scion Mg deficiency symptoms (A), sorted by increasing proportion of Mg deficient plants with a score 3 and 2, and rootstock classification based on petiole mineral content (B), sorted by increasing proportion of Mg deficient plants.

*Rootstocks in italics have been classified differently depending on the measurement used.

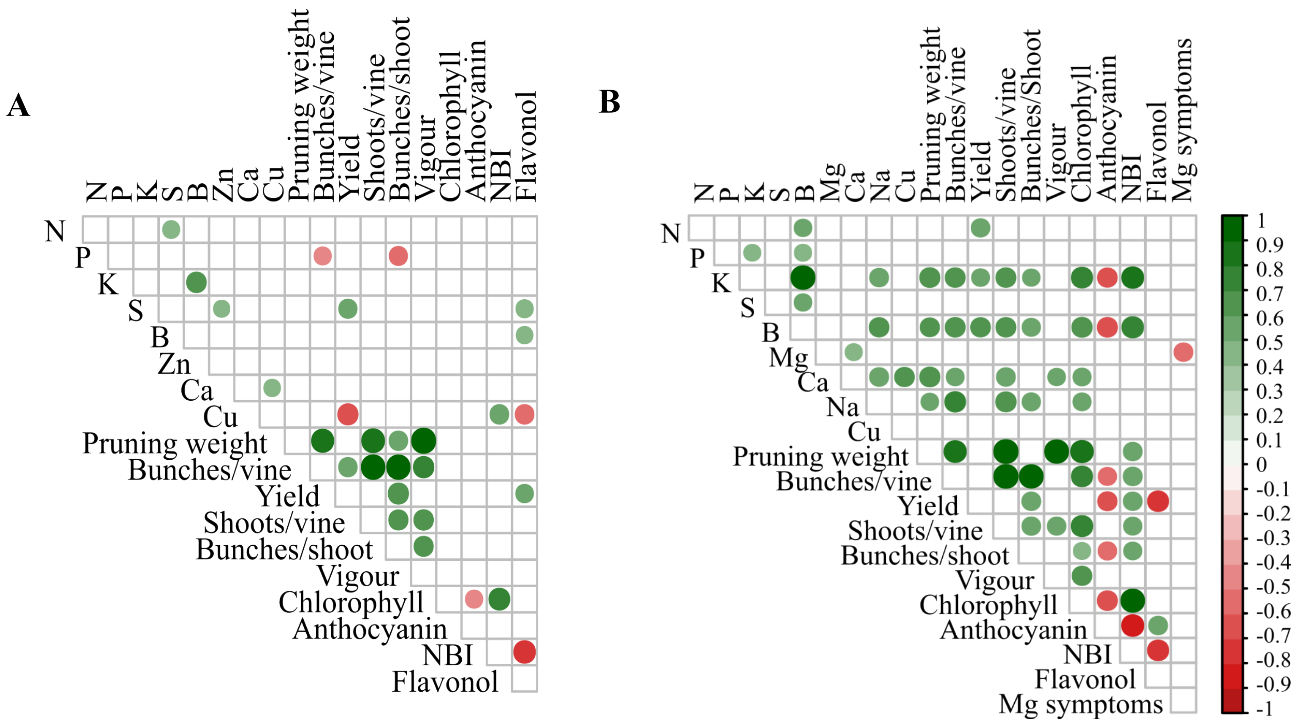

FIGURE 7. Correlation matrix of petiole mineral content, and growth- and yield-related traits in 2020 (A) and 2021 (B).

*Only significant correlations with R > 0.4 are plotted on the matrix.

There were fewer significant correlations between growth and vigour-related traits and mineral content in 2020 than in 2021 (Figure 7). In 2021, even though K content of most of the individuals was in excess (> 2.5 %), there were positive significant correlations between petiole K concentration and growth or yield-related traits (Figure 7.B) such as pruning weight or number of bunches (Supplementary Figure 3). Concerning B concentrations, most of individuals were in the optimum range (between 15 and 60 ppm), but there were also positive significant correlations between B and growth- and yield-related traits (Figure 7), such as pruning weight (Supplementary Figure 4.A) or number of bunches (Supplementary Figure 4.B).

DISCUSSION

This study is the most exhaustive in terms of the number of rootstocks and scions studied in the vineyard over two years. It allowed us to quantitatively determine the hierarchy of the rootstock and scion effects on mineral content of the petioles and to propose a rootstock classification of the Mg status of young grapevines in the vineyard (from 5 to 6 years old).

1. The effect of the rootstock on mineral composition was strong and stable over the two-year study

In a large panel of 55 rootstocks grafted with four different scion genotypes, the effect of rootstock on most of the petiole macroelement concentrations was significant and stable over the two years; similar results have been previously reported by Ibacache and Sierra (2009) and Verdugo-Vásquez *et al.* (2021). When comparing own-rooted Sultana and Sultana grafted onto four rootstock genotypes under different salinity treatments, Downton (1985) also found the patterns of element accumulation in leaves to be similar during both growing seasons of the study. Provost *et al.* (2021) studied Mg deficiency symptoms over six years in three scion varieties that had been either own-rooted or grafted with four rootstocks; they did not find a year effect, and the rootstock and scion effects were stable across the years. However, when more years are compared, differences can be found from year-to-year, for example when comparing leaf and must K concentrations between very dry and more humid years (Brancadoro *et al.*, 1995).

In general, N is usually the mineral element in the petiole that is the least affected by the rootstock (Kamiloğlu, 2022), and this was confirmed in our study. We also demonstrated the rootstock to have a large and stable effect on K and Mg, as was found in a study by Dalbó *et al.* (2011), although the range of petiole content values was higher in our case. Harris *et al.* (2021) found the rootstock effect on K and Mg to be low, but they showed a higher rootstock effect on Mg than on K. In our study, we confirmed this relative difference between these two elements over the two years. We also demonstrated that rootstock effect on other elements of interest, such as P and Ca, can be strong and stable, because we studied a wide range of rootstock.

However, the three-way interaction between the block, scion and rootstock factors explained a significant and non-negligible percentage of the variance. This complex relationship, involving all three factors simultaneously, and thus intricate interplay and potential underlying mechanisms, is difficult to interpret.

2. The genetic background conferred different mineral status over both years

Previous studies on the effect of rootstock genetic background on scion mineral composition have only been carried out on smaller numbers (< 15) of rootstock genotypes (Gautier *et al.*, 2020; Wolpert *et al.*, 2005), using either one scion (Gautier *et al.*, 2020) or multiple scions on different sites (Wolpert *et al.*, 2005). Therefore, it is difficult to relate rootstock genetic background to a scion mineral content when only few rootstocks are studied. Here we characterised the effect of rootstock genetic background across 47 rootstock genotypes grafted with four scion genotypes on one site using chi² analysis.

The rootstocks with a dominant *V. riparia* genetic background had a significantly higher proportion of plants with Mg or P deficiency and a significantly lower proportion of plants with Mg or P excess. The behaviour of the *V. riparia* genetic background was stable from the first study year to the next, and these results confirm the effect of genetic background on P petiole content that were previously reported Gautier *et al.* (2020).

V. berlandieri genetic background has been shown to induce low petiole K concentrations at bloom, but not at veraison (Wolpert *et al.*, 2005). We observed less K excess and more K deficiency in petioles at veraison for *V. berlandieri* and *V. berlandieri* × *V. vinifera* genetic backgrounds compared to the other genetic backgrounds. These slight differences could be due to the number of rootstocks studied, the scion genotypes and/or the local environmental conditions.

Although we studied a panel of 55 rootstock genotypes, the diversity within a given genetic background was limited, because the breeders of these rootstocks selected a limited range of parents (Maul *et al.*, 2023; Riaz *et al.*, 2019). The genetic diversity within a species can depend on the species being considered, but in general the diversity between genetic backgrounds is higher than the diversity within a genetic background (Peros *et al.*, 2021). Peros *et al.* (2021) studied three different species (*V. riparia*, *V. cinerea* and *V. aestivalis*) and showed that within-species diversity depends on the given genetic background. In the case of mildew resistance, a large variation in resistance was shown in each species, but *V. riparia* had a lower diversity than the other two species. This within-species diversity can be high: the diversity of root traits across 286 *V. berlandieri* genotypes can be higher than between the genetic backgrounds commonly used in rootstock breeding; i.e., *V. berlandieri* × *V. riparia*, *V. berlandieri* × *V. rupestris* and *V. riparia* × *V. cinerea* (Blois *et al.*, 2023).

3. Mineral petiole content at mid-veraison did not reflect mineral satiety of the plant

The evaluation of Mg status by combining tissue analyses and observation of deficiency symptoms has been carried out on different scion genotypes (Pedò *et al.*, 2019): for some genotypes, Mg deficiency was confirmed by visual symptoms but not by mineral concentrations. However, the effect of rootstock on the relationship between petiole Mg concentration and Mg deficiency symptoms observed on leaves has not yet been quantified. We found that the current satisfactory Mg status thresholds were suitable for most of the rootstocks; for example, scions grafted onto 44-53M, which is a well-known rootstock for a low Mg uptake (Cordeau, 1998; Ibacache *et al.*, 2020), had both low Mg petiole status and showed visual Mg deficiency symptoms.

However, there were some rootstocks for which the symptoms-based classification did not respect the classification obtained by petiole content. For example, Vialla showed a low Mg content, below the optimum threshold in both 2020 and 2021, but only a few plants (< 20 %) expressed strong Mg deficiency symptoms. Similarly, some rootstocks, such as 5BB, had an optimum level of Mg content, but more than 40 % of the plants expressed strong Mg deficiency symptoms, highlighting different levels of mineral satiety for rootstocks. The 5BB rootstock has previously been described as conferring medium Mg concentrations (Cordeau, 1998) and being susceptible to Mg deficiency (Ibacache *et al.*, 2020); this difference in categorisation can be explained by the difference between mineral petiole analysis and the symptoms observed. Ibacache *et al.* (2020) also evoked this difference between petiole content and symptoms in 110R, but it is difficult to know whether these differences were actually investigated for all rootstocks. The relationship between tissue mineral concentrations and tolerance to deficiency is not always easy to interpret; for example, when comparing Mg concentrations in tolerant (1103P) and sensitive (SO4) rootstocks, Livigni et al. (2019) found that the sensitive genotype had higher root and shoot Mg content that the tolerant genotype. In summary, the results of our work indicate that when making fertilisation choices rootstock must be taken into account and the optimal Mg thresholds should be reconsidered depending on the rootstock being studied.

4. K and Mg content in the petiole were not correlated, indicating a variability in K/Mg antagonism

Antagonism between K and Mg with respect to their uptake in plants is well known (Marcelin, 1977). The inhibition of Mg by K during their uptake by grapevine rootstocks was first observed in an *in vitro* experiment on cuttings of two Mg deficiency sensitive (44-53M and Fercal) and two Mg deficiency tolerant (41B and 140Ru) rootstocks by Bouquet *et al.* (1990). However, in the present study, we did not observe a negative relationship between K and Mg petiole concentrations in the diverse rootstocks studied. This may be due to the wide range of K/Mg ratios (0.5 to 60) (although K was most often in excess), or to the different degrees to which K inhibits Mg uptake, which has previously been shown for certain rootstocks (Ruhl, 1991).

As previously mentioned, many rootstocks in our study had low Mg and high K concentrations; i.e. the K/Mg ratio was highly imbalanced (> 10, such as in 44-53M and SO4).

The behaviour of these rootstocks has also been described in other studies (Cordeau, 1998; Ibacache *et al.*, 2020). Nevertheless, there were also rootstocks, such as 1103P, which had high K and high Mg concentrations; a result previously obtained by Scienza *et al.* (1986). The Schwarzmann rootstock had one of the lowest K and Mg concentrations over the two years; this rootstock is known for having a low Mg and K uptake ability (Ibacache *et al.*, 2020). Ibacache *et al.* (2020) suggested that 110R and 99R also had low K and Mg uptake capacities; however, these rootstocks did not show low K and Mg concentrations in our study or that of Cordeau (1998). Cultivation practices (e.g., drip irrigation vs rainfed vineyard) and scions (table grapes vs wine grapes) may explain these differences.

5. Growth- and yield-related traits are more impacted by K-excess than by Mg-deficiency

This is the first time that positive correlations between petiole K concentration and growth- and yield-related traits have been observed, even though there was an excess of K in all the plants. In previous studies, correlations have been found between K content in the soil, petiole K content, must pH and productivity-related traits (Assimakopoulou and Tsougrianis, 2012; Kodur, 2011). These studies focused more on berry quality and the link with oenological characteristics, whereas our study focused on the roles of the rootstock and scion, and their impact on plant development.

There were also correlations between petiole B concentrations and growth- and yield-related traits, although all plants had B contents within the optimum status range. Thus, we observed phenotypic variability, even though the plants had the same mineral status. This may be explained by the fact that the plants did not reach their physiological optimum. The variability observed could be due to the genetic variability of the rootstocks. B is known to be one of the essential micronutrients for the optimum growth, development, yield and quality of crops (Brown *et al.*, 2002).

The Mg deficiency due to the excess of K had no negative impact on the biomass or yield in our conditions; i.e., those of a K well-supplied vineyard (Supplementary Table 2). In a high productivity context (from 5 to 20 tons/ha), Tecchio *et al.* (2006) showed a negative correlation between Mg-content and yield, with most of the plants having an Mg deficiency status (as determined via petiole analysis). Assimakopoulou and Tsougrianis (2012) also found a negative correlation between Mg content and yield, but the actual Mg contents were not presented in their study. This suggests that production context (water status, fertiliser management and yield) largely influences the range of Mg-content in the petiole and the impact on yield and growth-related traits.

CONCLUSION

This study is the first to consider such a large panel of grafted rootstock varieties, in the field in a natural situation of Mg deficiency induced by K excess, in which visual observations and petiole analyses are combined. The effects of the rootstock on mineral composition, as well as of the genetic backgrounds on mineral status, were strong and significant over the two years, and particularly on macroelement concentrations. The mineral status thresholds currently used are generally relevant, but this study highlighted that petiole mineral content at mid-veraison does not always accurately reflect the mineral deficiencies observed, depending on the rootstock. In a K-excess context, this work also demonstrated the genetic variability of rootstock in terms of K/Mg ratio: there was no correlation between K and Mg content in the petiole. Growth and yield-related traits are more impacted by K-excess than by Mg-deficiency. As a result of this study, we were able to modify the classification of rootstocks for conferred K and Mg status in the scion; this could be useful for adapting choice of rootstock to soil characteristics or fertiliser management, and vice versa.

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