

Influence of the three main genetic backgrounds of grapevine rootstocks on petiolar nutrient concentrations of the scion, with a focus on phosphorus

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ABSTRACT

Background and aims: In most viticultural areas of the world, *Vitis vinifera* grapevines require grafting onto phylloxera-tolerant rootstocks of American origin. The species most commonly used in rootstock creation are *Vitis berlandieri*, *V. riparia* and *V. rupestris*. Rootstocks not only provide tolerance to phylloxera but also ensure the supply of water and mineral nutrients to the scion. The aim of the study was to investigate the extent to which rootstocks with different genetic backgrounds modify the mineral composition of the petioles of the scion.

Methods and results: *Vitis vinifera* cv. Cabernet-Sauvignon grapevines were grafted onto rootstocks of 13 different genotypes and planted in a vineyard in three blocks. Petiolar concentrations of 13 mineral elements at veraison (berry softening) were determined. The genetic background of the rootstock had significant effects on the mineral composition of the petioles. Use of rootstocks with a genetic background including at least one *Vitis riparia* parent decreased the concentration of phosphorus and magnesium and increased the concentration of sulphur in the petioles of Cabernet-Sauvignon.

Conclusion: Rootstocks with a *Vitis riparia* genetic background confer low petiolar concentrations of phosphorus and magnesium, and conversely, high petiolar concentration of sulphur.

Significance of the study: The kind of rootstock onto which a grapevine has been grafted is known to influence the nutrient content of the scion. The results of the study show a significant relation between the genetic background of a rootstock and its ability to modify concentrations of phosphorus, magnesium and sulphur in the petioles of the scion under field conditions.

KEYWORDS

nutrient, petiole, scion, *Vitis berlandieri*, *Vitis riparia*, *Vitis rupestris*, *Vitis spp.*

INTRODUCTION

Grafting is a horticultural technique that has been used for millennia (Mudge *et al.*, 2009) and is still practised today in the cultivation of perennial fruit crops (e.g. citrus fruit, apple, peach, cherry and grape) and annual fruits and vegetables (e.g. watermelon and tomatoes). It enables the desirable traits of two different genotypes to be combined in the same plant. Use of rootstocks affects plant vigour, phenology, resistance to pests, fruit quality, yield, and tolerance to deleterious environmental conditions such as water deficit and nutrient limitations (Warschefsky *et al.*, 2016).

The accidental introduction of the American aphid pest *Phylloxera* to Europe in the nineteenth century caused the near destruction of the European vineyard, because of the lack of phylloxera tolerance of roots of the Eurasian grapevine species *Vitis vinifera*. However, scientists of the time quickly realized that naturally resistant *Vitis spp.* of North American origin were the solution to the crisis. To maintain wine production in Europe and cater to the taste expectations of consumers, European *Vitis vinifera* varieties were grafted onto American *Vitis spp.* to combine fruit quality with phylloxera tolerance.

There are about 30 different American *Vitis spp.*; however, only a limited number have been used to breed rootstocks. In fact, most rootstocks used in viticulture are the result of breeding between just three different American *Vitis spp.* originating from different geographical areas: *V. riparia*, *V. rupestris* and *V. berlandieri* (Supplementary figure 1). According to the *Vitis* International Variety Catalogue database (<http://www.vivc.de>), 47 % of the 83 rootstocks used in Europe are the result of interspecies crosses of *Vitis berlandieri*, *V. riparia* and *V. rupestris*. Additionally, all rootstocks used in Europe have at least one of these three *Vitis spp.* in their genetic background (47 % with *V. berlandieri*, 52 % with *V. riparia*, and 30 % with *V. rupestris*). Furthermore, the potentially high genetic variability of American *Vitis spp.* is poorly exploited, because it is estimated that 90 % of *Vitis vinifera* plants in the world are grafted onto rootstocks of fewer than 10 different genotypes (Galet, 1988; Huglin and Schneider, 1998; Keller, 2015; Ollat *et al.*, 2016). Therefore, there is considerable scope to improve current grapevine rootstock breeding programmes, to select not only for tolerance to phylloxera but also for various other agronomical traits, such as adaptability to soil properties or environmental conditions, resistance to other soil pathogens,

and ability to control scion vigour (as defined by extent of shoot growth) (May, 1994; Keller, 2015).

Roots acquire mineral nutrients and water from the soil, anchor plants in the ground, and interact with soil organisms. Plants require at least 14 mineral elements for adequate development, most of which are mainly taken up by the roots from the soil solution (Marschner, 2011). They include the macronutrients nitrogen (N), phosphorus (P), potassium (K), calcium (Ca), magnesium (Mg) and sulphur (S), and the micronutrients chlorine (Cl), boron (B), iron (Fe), manganese (Mn), copper (Cu), zinc (Zn), nickel (Ni) and molybdenum (Mo). These are required in different proportions, and deficiency or excess (toxicity) of any one of them reduces plant growth and crop yields. Numerous reviews have highlighted the facts that mineral homeostasis is highly regulated in plants and that the metabolism of different elements is interconnected (Amtmann and Armengaud, 2009; Williams and Salt, 2009). Additionally, in perennial species the root system is a storage organ for carbohydrates and other nutrients needed for the resumption of growth in the spring (Richards, 1983).

Differences in the mineral composition of plants may be due to genotypic factors responsible for differences in the nutrient- and water-uptake capacities of the roots, mobilization of stored nutrient reserves, allocation of nutrients and water within the plant, efficiency of nutrient use, and growth (all of which alter concentrations of mineral elements via dilution). The ability of a root system to take up nutrients or water is also related to development of the root system, its distribution in the soil (i.e. shallow or deep exploration), and its interactions with the rhizosphere (Dakora and Phillips, 2002; Lambers *et al.*, 2006). Plant mineral composition is also affected by external factors, mainly soil structure and composition, nutrient availability and climatic conditions. Plants modify the pH of the rhizosphere and release various compounds (e.g. hormones, carboxylates and enzymes) that affect microbial activity or nutrient availability in the soil. Consequently, plant mineral composition is related to interactions between genotype and environment as well as the relative plasticity of plant development in response to nutrient availability.

In many grafted crops, vegetative growth and the mineral composition of the scion are strongly affected by the rootstock (as reviewed recently by Nawaz *et al.*, 2016). In grapevine, rootstocks have long been known to modify the mineral

element profile of the scion (Cordeau, 1998; Bavaresco and Pezzutto, 2003). Ibacache and Sierra (2009) investigated N, P and K content in the petioles of four scion cultivars (*Vitis vinifera*) grafted onto 10 different rootstocks; they showed rootstock effects on concentrations of N, P and K in the scion. Furthermore, several studies have shown differences in the response of grapevine rootstocks to the supply of nutrients such as N (Lecourt *et al.*, 2015; Cochetel *et al.*, 2017), P (Grant and Matthews, 1996a; Grant and Matthews, 1996b; Gautier *et al.*, 2018), K (Ruhl, 1989; Ruhl, 1991) and Fe (Covarrubias and Rombolà, 2015; Covarrubias *et al.*, 2016). In these studies, grapevine rootstocks with different genetic backgrounds showed different responses to low nutrient supply.

Despite the considerable agronomical knowledge regarding the influence of rootstock on the mineral composition of the scion, few studies have shown a strong relation between rootstock genetic background and scion mineral composition in grapevine (Wolpert *et al.*, 2005). In the present study, we characterized the effects of rootstock genetic background on the elemental composition of scion petioles by means of an experiment in which grapevines were grafted onto rootstocks of many different genotypes and grown under non-nutrient and water-limited field conditions.

MATERIALS AND METHODS

1. Vineyard site and experimental design

In 2014, *Vitis vinifera* cv. Cabernet-Sauvignon clone 169 was omega-grafted onto rootstocks of 13 different genotypes and then grown in a nursery for 1 year. The rootstocks were RGM, 3309C, 101-14MGt, 420A, SO4, 44-53M, Gravesac, Freedom, Dog ridge, Rupestris du Lot, 1103P, 110R and 41B. This panel was sufficiently diverse to include representatives from the three main American *Vitis* spp. used in rootstock crosses (i.e. *V. riparia*, *V. rupestris* and *V. berlandieri*). The rootstocks and their genetic backgrounds are summarized in Supplementary table 1. The experimental vineyard was planted in 2015 with three blocks of five grapevines per block for each rootstock.

The experiment was carried out during the 2017 season in an experimental vineyard near Bordeaux, France (44°47'N, 0°34'W; elevation, 22 m) with a row spacing of 1.5 x 1 m (6666 vines/ha). Vines were winter-pruned to 3–5 buds per vine on Guyot simple and trained to a vertical trellis system.

Canopy management practices included shoot hedging. Mean canopy height and width were about 1.6 and 0.4 m, respectively. The soil at the site was a gravelly sandy soil. Mean cation exchange capacity was 3.2 cmol+/kg, and available water capacity was 0.85 mm/cm. Phosphorus content was 0.015 %, which is about average for the type of soil. The soil was not tilled during the experiment; weeds appearing between rows and in the vine row were controlled by mowing several times a year (additional information on soil profile is given in Supplementary table 2).

2. Growth measurements

Annual growth of each vine was evaluated by quantifying winter cane pruning weight at the end of 2017. For each different rootstock, the cane pruning weights of five grapevines in each of the three blocks were measured (i.e. 15 grapevines per rootstock genotype).

3. Mineral analysis

For each different rootstock, four petioles were collected at veraison (berry softening, 14 August 2017) from two plants in each block (i.e. eight petioles per rootstock genotype), with two replicates (i.e. two samples per block; n = 6). Petioles were harvested near to a bunch, from nodes 2 to 4, and were dried in an oven at 60 °C until a constant mass was achieved.

The mineral composition of the samples was analysed by Waypoint Analytical (Richmond, VA, USA). Nitrogen concentration was determined using a Leco FP-528 instrument (Leco, St Joseph, MI, USA). Concentrations of other elements (P, K, S, Mg, Ca, Na, B, Zn, Mn, Fe, Cu and Al) were determined by ICP-OES MS 730-ES (Varian, Palo Alto, CA, USA), using plant samples that had first been digested with nitric acid and hydrochloric acid in a CEM Mars5 microwave digester (CEM, Matthews, NC, USA). Concentrations are expressed in terms of percentage (weight/weight) or ppm.

4. Statistical analysis

All statistical analyses were done using R Statistics Environment (R Development Core Team, 2005). Rootstock effects on shoot growth and petiolar nutrient concentrations were determined by one-way analysis of variance (ANOVA; significance level $P < 0.05$ with Tukey's honest significant difference test) if the normality of residuals and the homogeneity of variances were respected (i.e. in the cases of cane pruning weight and

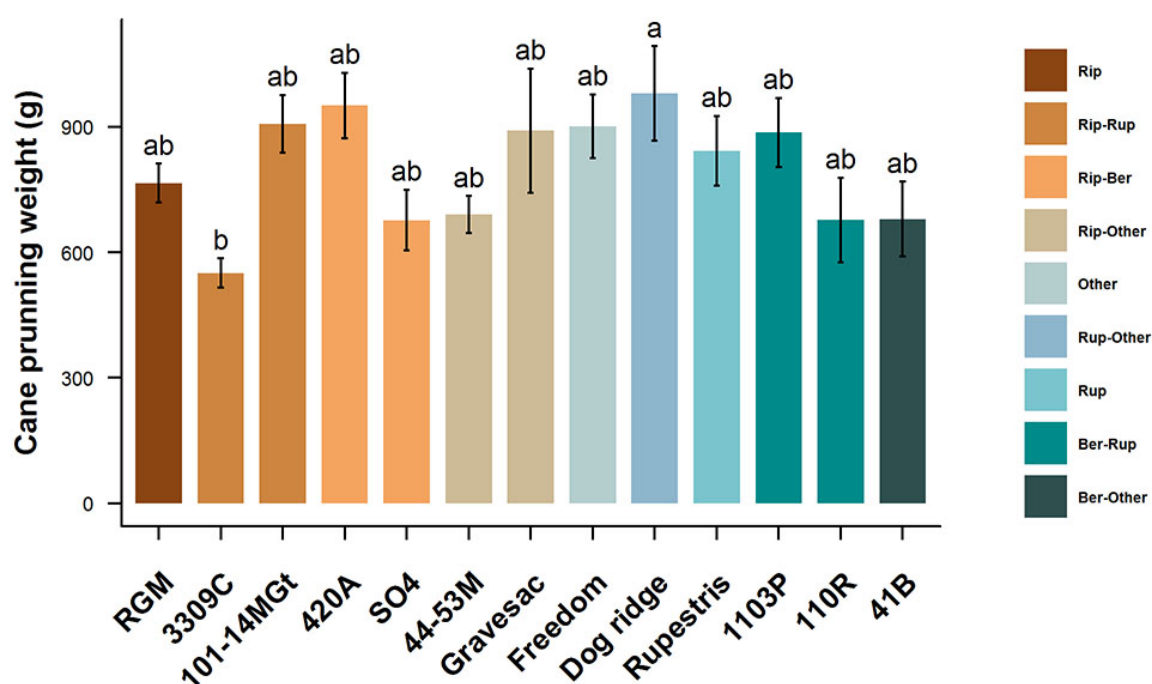


FIGURE 1. Winter cane pruning weight in 2017 for *Vitis vinifera* cv. Cabernet-Sauvignon grafted onto 13 different rootstocks.

The full name of each rootstock is given in Supplementary table 1. Bar colour indicates the genetic background of the rootstock: brown, *Vitis riparia* (Rip); dark orange, hybrids of *V. riparia* and *V. rupestris* (Rup); pale orange, hybrids of *V. riparia* and *V. berlandieri* (Ber); sand beige, other hybrids containing *V. riparia*; grey, hybrids of other *Vitis* spp.; light blue, other hybrids containing *V. rupestris*; turquoise, *V. rupestris*; green, hybrids of *V. rupestris* and *V. berlandieri*; and dark green, other hybrids containing *V. berlandieri*. Means and standard deviations are shown ($n = 6$). Different letters indicate significant differences at $P < 0.05$, tested by one-way ANOVA using rootstock genotype as a factor.

petiolar N, K, S, Ca, Cu and Al concentrations). When the conditions of an ANOVA were not met (i.e. in the cases of petiolar P, Mg, Na, B, Zn, Mn and Fe concentrations), the data were analysed using a Kruskal–Wallis test ($P < 0.05$). The effects of *Vitis riparia*, *V. rupestris* and *V. berlandieri* genetic backgrounds on mean petiolar mineral concentrations were tested, using t-tests (significance level, $P < 0.05$) with a Bonferroni multiple-testing correction. In the first comparison, data for rootstocks with a *Vitis riparia* genetic background (i.e. RGM, 3309C, 101-14MGt, 420A, S04, 44-53M and Gravesac) were compared with those for rootstocks without it. In the second comparison, data for rootstocks with a *Vitis rupestris* genetic background (i.e. 3309C, 101-14MGt, Dog ridge, Rupestris, 1103P and 110R) were compared with those for rootstocks without it. A third comparison was done by comparing data for rootstocks with a *Vitis berlandieri* genetic background (i.e. 420A, S04, 1103P, 110R and 41B) with those for rootstocks without it.

Principal component analysis was carried out on Pearson correlations, using the FactoMineR package.

RESULTS

1. Scion vigour was significantly affected by rootstock genotype

Petiolar elemental composition was analysed in Cabernet-Sauvignon grapevines planted in a 4-year old experimental vineyard. At this developmental stage, there were various significant differences in vigour ($P = 0.01$) between plants with different rootstocks (Figure 1). However, only 3309C conferred a significantly lower vigour than Dog ridge.

Two-way ANOVA was carried out to determine the potential effect of the different blocks of the experimental vineyard. The results showed that rootstock genotype explained 31.4 % of phenotypic variance, whereas block explained only 0.5 %.

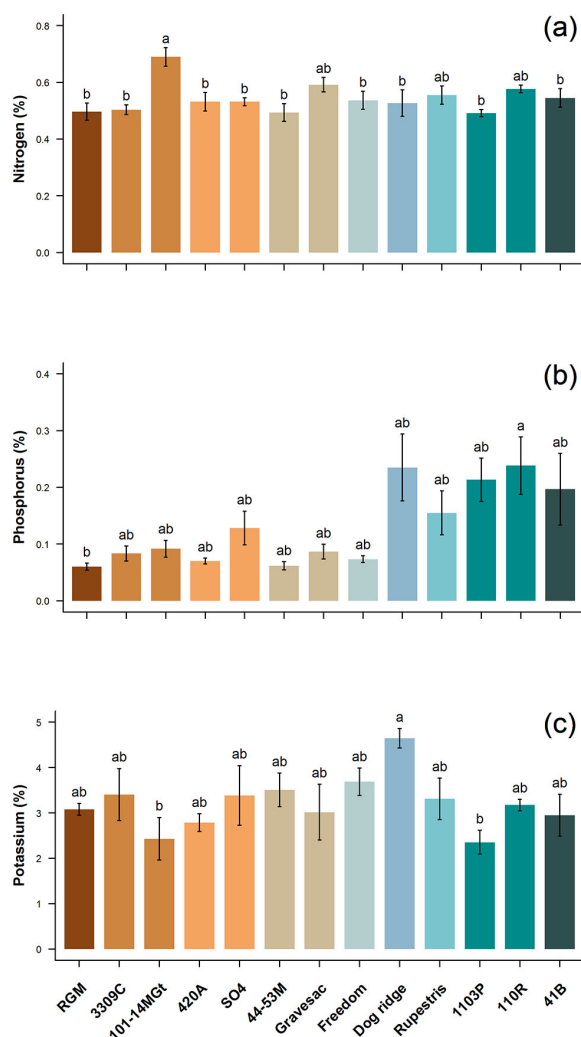


FIGURE 2. Petiolar concentration of (a) nitrogen, (b) phosphorus and (c) potassium in *Vitis vinifera* cv. Cabernet-Sauvignon grafted onto 13 different rootstocks.

The full name of each rootstock is given in Supplementary table 1. See the legend to Figure 1 for an explanation of the bar colour code. Means and standard deviations are shown ($n = 6$). Different letters indicate significant differences at $P < 0.05$, tested by one-way ANOVA (for N and K) or Kruskal–Wallis test (for P), using rootstock genotype as a factor.

2. Differences in petiolar mineral element composition were related to rootstock genotype

The petiolar concentration of each nutrient analysed, except Na, was significantly affected by rootstock genotype. The concentration of each of the three major mineral elements (i.e. N, P and K) varied significantly depending on the rootstock (Figure 2). Petiolar N concentration was significantly affected by rootstock genotype

($P = 0.0005$); 101-14MGt conferred the highest N concentration (0.69 %), whereas 1103P, 44-53M and RGM conferred the lowest (0.49 %) (Figure 2a). Petiolar P concentration was also significantly affected by rootstock genotype ($P = 0.0002$), varying 4-fold between the lowest concentration (for RGM) and the highest concentrations (for 110R and Dog ridge) (Figure 2b). It appeared to be related to the genetic background of the rootstock, being lower when the rootstock had a *V. riparia* parent and highest in hybrids without a *V. riparia* parent (Figure 2b). Petiolar K concentration was also affected by rootstock genotype ($P = 0.035$), varying more than 2-fold between the lowest concentrations (for 1103P and 101-14MGt) and the highest (for Dog ridge) (Figure 2c).

Petiolar concentrations of other macronutrients also varied depending on the rootstock (Figure 3). The petiolar concentration of both S and Mg was significantly different ($P = 6.3 \times 10^{-12}$ and $P = 1.2 \times 10^{-6}$, respectively), varying 3-fold between the highest concentration and the lowest (Figure 3a and 3b, respectively). The petiolar S concentration of grapevines grafted onto 101-14MGt was 0.17 %, versus about 0.06 % in those grafted onto 110R or 3309C (Figure 3a). Regarding petiolar Mg concentration, 44-53M conferred a lower concentration (0.23 %) than 1103P, 101-14MGt, 41B and Gravesac (about 0.75 %) (Figure 3b). In contrast, although petiolar Ca concentration was also affected by rootstock genotype ($P = 0.007$), it varied by less than 2-fold between the lowest concentration (2.03 % for 3309C) and the highest (3.45 % for Freedom) (Figure 3c). Petiolar Na concentration was unaffected by rootstock genotype ($P = 0.21$) (Figure 3d).

Petiolar concentrations of microelements were significantly affected by rootstock genotype (Figure 4). The effect on petiolar B concentration was significant ($P = 0.001$); RGM and 420A conferred lower concentrations (about 23 ppm), whereas Dog ridge and 110R conferred higher concentrations (about 30 ppm) (Figure 4a). The petiolar concentration of both Zn and Mn was also significantly affected by rootstock genotype ($P = 0.038$ and $P = 0.023$, respectively). For Zn, the difference was about 2-fold: grapevines grafted onto 110R had a petiolar concentration of 56 ppm, whereas those grafted onto Gravesac had a petiolar concentration of 102 ppm (Figure 4b). Petiolar Mn concentration showed the greatest variation, with a 20-fold difference between the lowest and highest values (45 ppm for 44-53 M versus 865 ppm for SO4). However, for both Zn

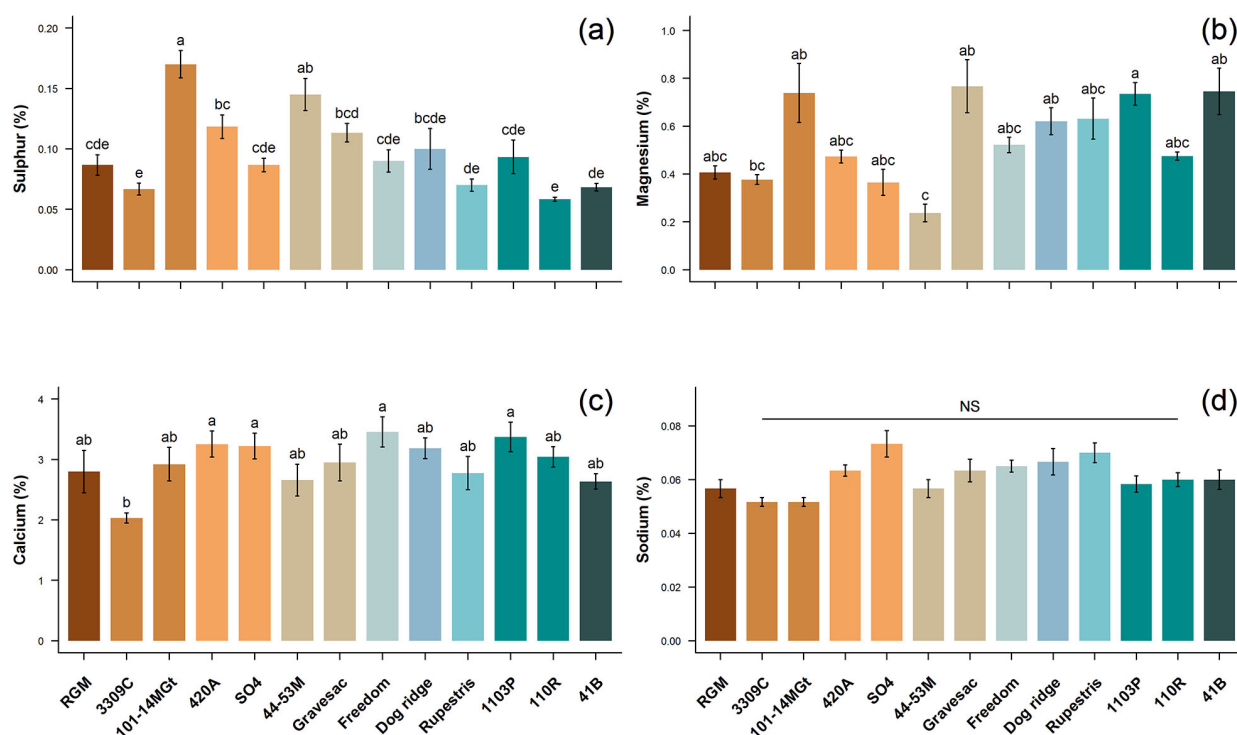


FIGURE 3. Petiolar concentration of (a) sulphur, (b) magnesium, (c) calcium and (d) sodium in *Vitis vinifera* cv. Cabernet-Sauvignon grafted onto 13 different rootstocks.

The full name of each rootstock is given in Supplementary table 1. See the legend to Figure 1 for an explanation of the bar colour code. Means and standard deviations are shown ($n = 6$). Different letters indicate significant differences at $P < 0.05$, tested by one-way ANOVA (for S and Ca) or Kruskal–Wallis test (for Mg and Na), using rootstock genotype as a factor.

and Mn, the Kruskal multiple comparison did not allow separation of different statistical groups (Figure 4b and 4c). Petiolar Fe concentration was significantly affected by rootstock genotype ($P = 2.1 \times 10^{-6}$), showing 3-fold variation between SO4 (17 ppm) and 101-14MGt (60 ppm) (Figure 4d). Regarding petiolar Cu concentration, several rootstocks (RGM, 110R, 44-53M, Rupestris du Lot and 420A) conferred lower concentrations (< 15 ppm), whereas 1103P and 41B conferred higher concentrations (> 20 ppm) ($P = 1.71 \times 10^{-6}$) (Figure 4e). Petiolar Al concentration also showed significant variation depending on rootstock genotype ($P = 2.18 \times 10^{-7}$). Dog ridge and Freedom conferred high Al concentrations (> 20 ppm), whereas 420A, 101-14MGt, 1103P, 44-53M and 3309C conferred low Al concentrations (< 12 ppm) (Figure 4f).

3. Rootstock genetic background influenced petiolar mineral concentration profile

Mineral concentration data were subjected to principal component analysis. The first two

principal components, PC1 and PC2, explained 19.9 % and 16.1 % of total variability, respectively (Figure 5). The positive values of PC1 are related to higher petiolar concentrations of P, Ca, Cu and Mg, whereas the negative values are related to higher petiolar concentrations of Mn, Zn, S and N. Furthermore, PC1 separated rootstocks with a *V. riparia* genetic background (negative values) from those without it (positive values). The positive values of PC2 are related to higher petiolar concentrations of K, Al, Na and B, whereas the negative values of PC2 are related to higher petiolar concentrations of Fe and Mg.

4. Pair-wise comparisons of the effect of *Vitis riparia*, *V. rupestris* and *V. berlandieri* parents on petiolar nutrient concentrations

The effects of the species most commonly used in rootstock creation (i.e. *Vitis riparia*, *V. rupestris* and *V. berlandieri*) on the mineral composition of scion petioles were investigated by comparing data for the concentration of each element in the petioles of grapevines grafted onto rootstocks

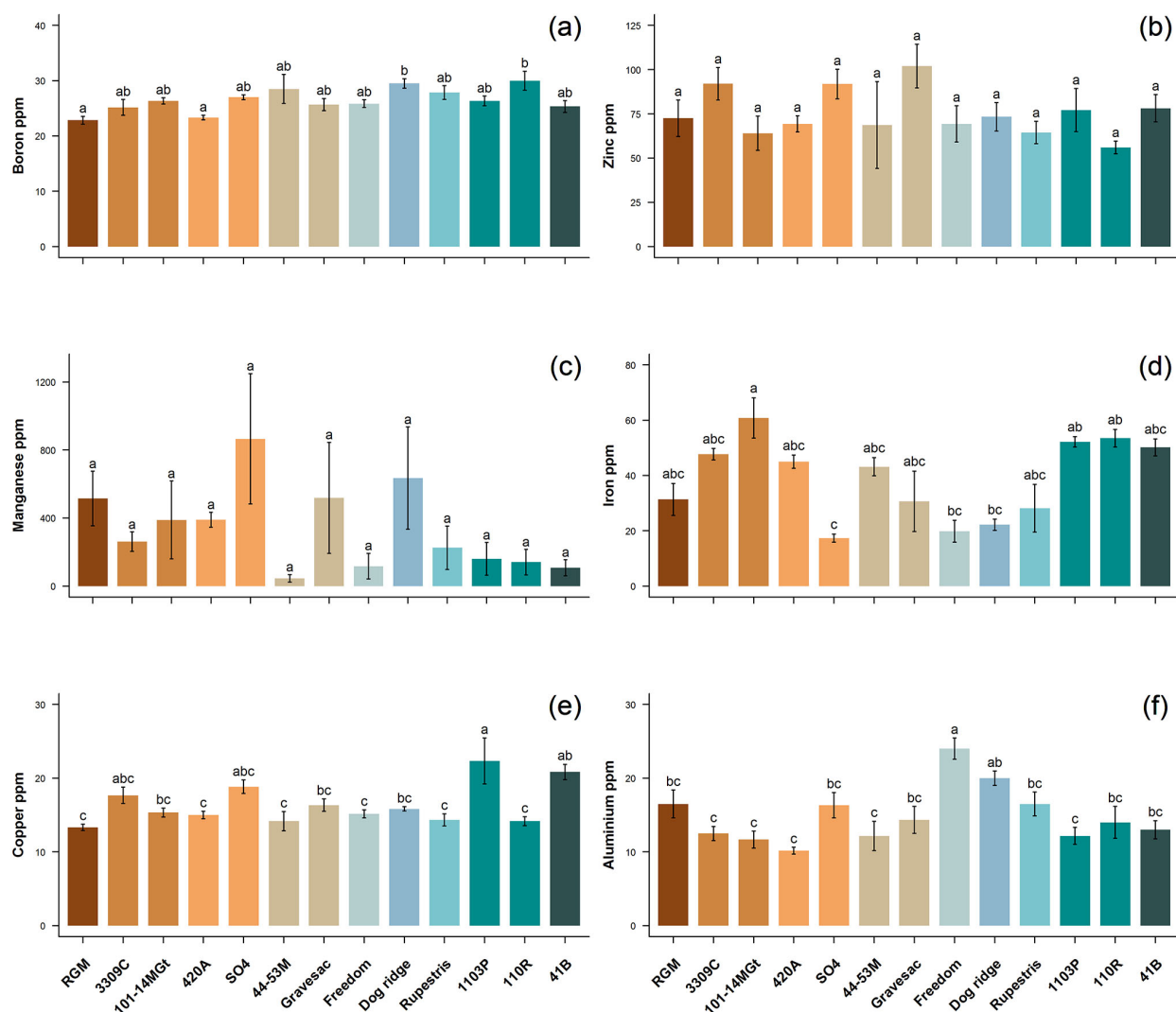


FIGURE 4. Petiolar concentration of the microelements (a) boron, (b) zinc, (c) manganese, (d) iron, (e) copper and (f) aluminium in *Vitis vinifera* cv. Cabernet-Sauvignon grafted onto 13 different rootstocks.

The full name of each rootstock is given in Supplementary table 1. See the legend to Figure 1 for an explanation of the bar colour code. Means and standard deviations are shown (n = 6). Different letters indicate significant differences at $P < 0.05$, tested by one-way ANOVA (for Cu and Al) or Kruskal–Wallis test (for B, Zn, Mn and Fe), using rootstock genotype as a factor.

DISCUSSION

1. Rootstocks influence petiolar mineral concentration

It is well known that in many grafted cultivated species, mineral nutrition is affected by rootstock genotype (Nawaz *et al.*, 2016). In the present study, carried out under non-limited mineral conditions, the mineral composition of Cabernet-Sauvignon petioles was affected by the rootstock; this result is consistent with the literature (Cordeau, 1998; Ibacache and Sierra, 2009). The mineral composition of scion petioles was related to rootstock genotype, with groupings based on the presence or absence of a *Vitis riparia*, *V. rupestris*

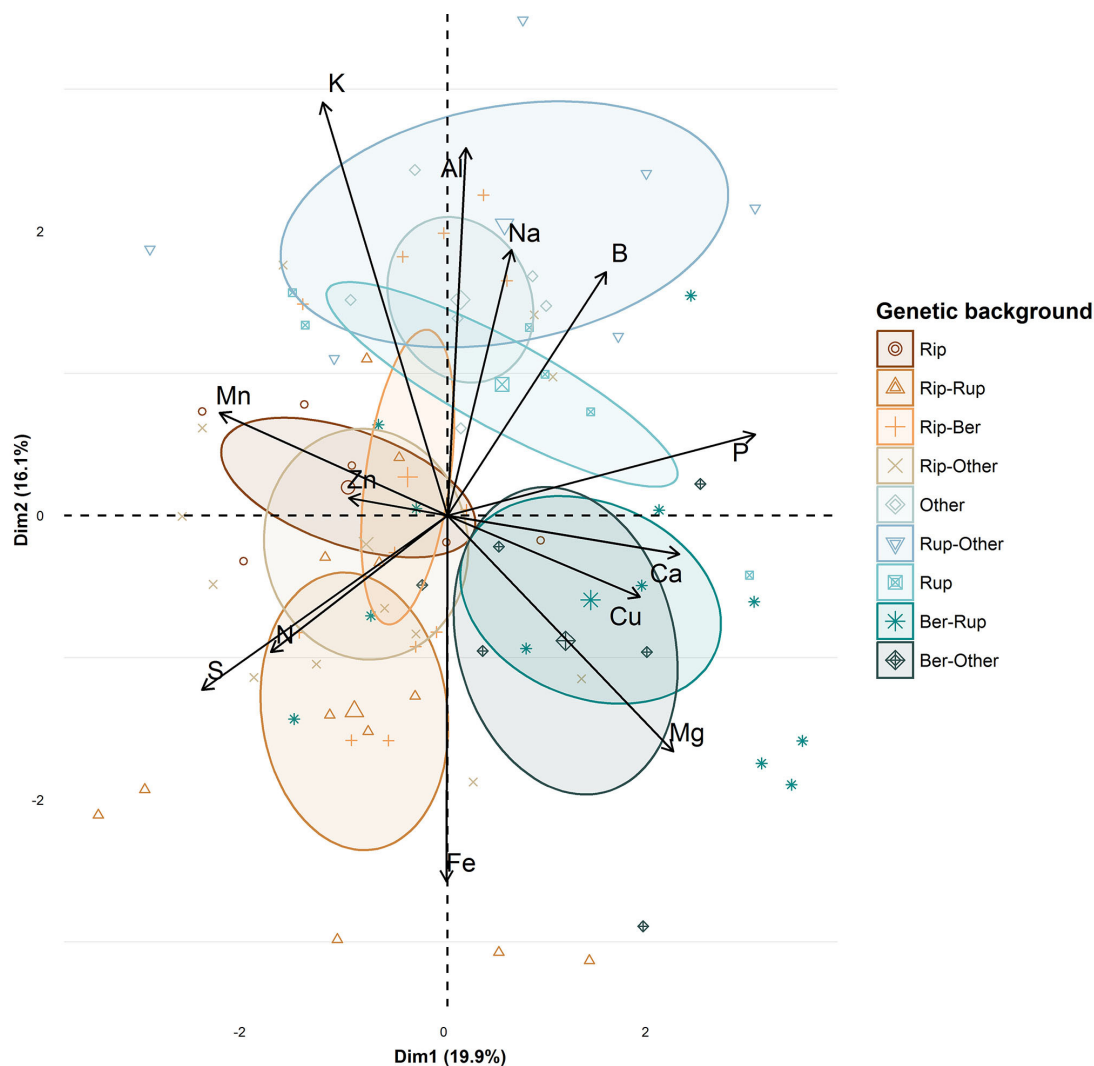


FIGURE 5. Principal component (PC) analysis of the petiolar concentrations of minerals in *Vitis vinifera* cv. Cabernet-Sauvignon grafted onto 13 different rootstocks.

The distribution of variables (mineral concentrations indicated by arrows) and individual observations (symbols) on PC1 and PC2 are shown. Ellipses of confidence at the 95 % level are given for each rootstock parentage. Ber, *Vitis berlandieri*; Rip, *V. riparia*; Rup, *V. rupestris*.

or *V. berlandieri* genetic background. This is the first time that, because of the use of such a large panel of rootstocks, the genetic background of rootstocks has been related to the mineral profile of the scion, although similar studies have been done for only K content in the petiole (Wolpert *et al.*, 2005), in ungrafted plants for variables associated with drought tolerance (Rossdeutsch *et al.*, 2016), and conferred vigour (Jones *et al.*, 2009).

2. The genetic background of rootstocks did not confer differences in scion vigour

In viticulture, vigour is often defined by the rate of shoot growth (Keller, 2015), and rootstocks

affect the vigour of the scion in many species, including grapevine (Zhang *et al.*, 2016). In grapevine, vigour is typically quantified by cane pruning weight at the end of the growing season, and rootstock-induced differences in scion development are often striking in mature plants growing in a vineyard (Jones *et al.*, 2009; Wooldridge *et al.*, 2010). In the present study, rootstock genotype affected cane pruning weight and explained 31.4 % of phenotypic variance; however, we were unable to show any significant differences between the results for rootstocks with different genetic backgrounds. The results of several studies and agronomical data from

TABLE 1. The effect of *Vitis riparia*, *V. rupestris* and *V. berlandieri* parents on mean cane pruning weight and petiolar mineral concentrations in the scion, tested using Student's t-test with the Bonferroni correction

Asterisks indicate significant differences between rootstock genetic background, using Student's t-test with the Bonferroni correction: *, $P < 0.5$; **, $P < 0.01$; ***, $P < 0.001$. Standard critical concentrations were added to confirm the absence of any deficiency (Delas, 2011).

	Shoot weight (g)	Petiolar concentration ^a												
		N	P	K	S	Mg	Ca	Na	B	Zn	Mn	Fe	Cu	Al
With <i>riparia</i> (n = 42)	776	0.548	0.083	3.086	0.112	0.48	2.833	0.059	25.54	80.04	421.6	37.67	15.81	13.38
Without <i>riparia</i> (n = 36)	791	0.586	0.185	3.353	0.08	0.621	3.077	0.063	27.47	69.75	230.5	39.42	17.11	16.61
<i>t</i> -test			***		***	**			*					**
With <i>rupestris</i> (n = 36)	807	0.557	0.169	3.219	0.093	0.596	2.888	0.059	27.53	71.17	301.6	44.08	16.61	14.47
Without <i>rupestris</i> (n = 42)	793	0.532	0.097	3.201	0.101	0.502	2.984	0.063	25.50	78.83	365.2	33.93	16.23	15.21
<i>t</i> -test			**						*			*		
With <i>berlandieri</i> (n = 30)	773	0.553	0.169	2.929	0.085	0.559	3.105	0.063	26.40	74.50	332.5	43.63	18.23	13.13
Without <i>berlandieri</i> (n = 48)	816	0.549	0.106	3.384	0.105	0.537	2.846	0.060	26.58	75.79	338.1	35.48	15.27	15.96
<i>t</i> -test			*		*							***	***	*
Standard critical concentration (of dry biomass) (Delas, 2011)		0.4–0.6 %	0.1–0.18 %	1.5–2.5 %		0.4–0.6 %	2–4 %		> 15 ppm	> 20 ppm	> 20 ppm			

^aExpressed as percentage (weight/weight) for N, P, K, S, Mg, Ca and Na, and as ppm for B, Zn, Mn, Fe, Cu and Al.

vineyards have shown that rootstocks with a *Vitis rupestris* or *V. berlandieri* genetic background confer a higher of scion vigour than rootstocks with a *V. riparia* genetic background (Galet, 1988; Cordeau, 1998; Galet and Smith, 1998; Bettiga, 2003). However, such differences were not found in the present study. Given that the plants were only 4 years old, differences will probably appear over time. Woody perennial species such as grapevine generally require a number of years between grafting and reproductive (and fully productive) maturity.

3. The genetic background of rootstocks conferred significant differences in petiolar P concentration

In the present study, the presence of a *Vitis riparia* parent in the genetic background of a rootstock reduced the concentration of P in the petioles of the scion, whereas that of a *V. rupestris* or *V. berlandieri* parent increased it. The results of agronomical studies have previously shown that *Vitis riparia* cv. RGM reduces petiolar P concentration (Cordeau, 1998). Experiments in pots have also shown that RGM reduces shoot P concentration (except under very high N supply) in comparison with the *Vitis rupestris* x *V. berlandieri* hybrid cv. 1103P when grafted to Cabernet-Sauvignon (Lecourt *et al.*, 2015). Using ungrafted cuttings, we have previously shown that RGM is less efficient than 1103P in terms of P uptake and P remobilization from perennial woody parts during the initial stages of grapevine development (Gautier *et al.*, 2018). In the present study, we have shown that the presence of only one *Vitis riparia* parent also confers this low P concentration phenotype.

Differences in P acquisition and use between *Vitis riparia* and other *Vitis spp.* could be related to their geographical origin. *Vitis riparia* has a large geographical range, being found across most of North America. In comparison, other *Vitis spp.* used for rootstock breeding, such as *V. rupestris*, *V. berlandieri*, *V. cordifolia*, *V. longii* and *V. candicans* have a more limited geographical range (Galet, 1988). *Vitis rupestris* and *V. berlandieri* are native to the south of the USA (Galet, 1988), particularly Texas, where soil is calcareous and often deficient in P due to precipitation of calcium phosphate (McLean, 1973). These species may have acquired efficient mechanisms to increase P acquisition or use in response to the limited-P environment.

4. Petiolar P concentration correlates with known vigour conferred by the rootstock

Phosphorus is an essential element for plant growth (Bieleski, 1973). It is involved in many fundamental processes, including photosynthesis, biosynthesis and respiration, because of its role in energy generation via adenosine triphosphate. Additionally, P has a structural role in phospholipids and phosphate esters (Marschner, 2011). Reduction in growth of the shoot is a typical response to P starvation in plants (Vance *et al.*, 2003; Hermans *et al.*, 2006). The results of agronomical studies carried out in a Bordeaux vineyard have previously shown that grapevine rootstocks that confer high vigour to the scion also confer high petiolar P concentration in the scion at veraison (Cordeau, 1998). However, in these studies, the influence of the age of plants, soil characteristics and agricultural practices were not considered. In the present study, no differences in rootstock-conferred vigour were found, for the reasons described above. However, rootstocks (with a *Vitis riparia* genetic background) that confer low vigour to the scion in a mature vineyard also confer low P concentrations, when compared with *V. rupestris* and *V. berlandieri* hybrids.

5. Rootstocks with a *Vitis riparia* genetic background have increased petiolar S concentration

In addition to reducing petiolar P concentration, use of rootstocks with at least one *Vitis riparia* parent also increases petiolar S concentration. The interaction between P and S nutrition is well known; under conditions of P deficiency, phospholipids are replaced by sulpholipids, and conversely, under conditions of S deficiency, sulpholipids are replaced by phospholipids (Essigmann *et al.*, 1998; Härtel *et al.*, 1998; ; Yu *et al.*, 2002; Sugimoto *et al.*, 2007). We have previously shown that the P acquisition efficiency of cuttings of RGM is lower than that of 1103P (Gautier *et al.*, 2018). This may suggest that *Vitis riparia* rootstocks are less able to take up P from the soil, which could induce a compensatory increase in S uptake and transport to the scion.

6. Rootstocks with a *Vitis riparia* genetic background confer low petiolar Mg concentration

Petiolar Mg concentration of Cabernet-Sauvignon was affected by rootstock genotype. In some cases, grapevines show symptoms of Mg deficiency, and the rootstock 44-53M has previously

been described as being associated with low Mg acquisition capacity (Cordeau, 1998). In agreement with the literature, 44-53M conferred the lowest petiolar Mg concentration in the present study. Furthermore, rootstocks with a *Vitis riparia* genetic background conferred lower petiolar Mg concentration than rootstocks without it. In the present study, petiolar P and Mg concentrations were positively correlated (Pearson correlation coefficient, 0.34), suggesting an interaction between P and Mg assimilation in grapevine.

In California, grapevines with symptoms of Mg deficiency have been found on low-P soils (Skinner *et al.*, 1988). Skinner *et al.* (1988) showed that grapevines growing under conditions of low P supply showed symptoms of Mg deficiency that were relieved by application of P fertilizer. In the present study, compared with other rootstocks, those with a *Vitis riparia* genetic background conferred lower petiolar P concentration. This is presumably linked to a lower capacity to take up P from the soil (Gautier *et al.*, 2018). This lack of P-uptake capacity could also affect uptake of Mg by rootstocks with a *Vitis riparia* genetic background and its subsequent translocation to the shoots.

CONCLUSION

Grapevine rootstocks have long been known to modify the mineral profile of the scion. However, the mechanisms underlying this phenomenon are poorly understood. For the first time, the capacity of different rootstocks to influence petiolar P concentration has been shown to be associated with the genetic background of the rootstock.

Phosphorus was the major mineral element differentially accumulated in the petiole in response to rootstock genotype. Petiolar P concentration was reduced when rootstocks with a *Vitis riparia* genetic background were used. Conversely, it was increased when rootstocks with a *Vitis rupestris* or *V. berlandieri* genetic background were used. Rootstocks with a *Vitis riparia* genetic background generally confer a lower level of vigour to the scion, whereas those with a *V. rupestris* or *V. berlandieri* background confer higher vigour. Therefore, the results may suggest that P nutrition corresponds to rootstock-conferred vigour in grapevine. Additionally, the poor efficiency of P uptake from the soil and of P remobilization from the perennial woody tissues of *Vitis riparia* (Gautier *et al.*, 2018) may indirectly influence the concentration of other nutrients, such S and Mg.

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