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Genetic architecture of root related traits and scion responses induced by grapevine rootstock: First study in a monospecies population of *Vitis berlandieri*

Louis Blois

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Genetic architecture of root related traits and scion responses induced by grapevine rootstock

First study in a monospecies population of *Vitis berlandieri*

Architecture génétique des traits racinaires et des réponses du greffon induites par le porte-greffe de vigne

Première étude chez une population mono-spécifique de *Vitis berlandieri*

submitted by

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In fulfilment of the requirements of a Doctorate under international joint supervision
leading to the award of a double degree

Doktor der Agrarwissenschaften (Dr. agr.)

and

Docteur de l'université de Bordeaux

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Abstract

English

In the context of climate change, crop adaptation is of major interest. Adaptation can be achieved by modifying cultural practices, field management, or plant material. In grafted plants, the plant material can be improved by the scion or the rootstock. The rootstock comprises the anchorage and the nutrient and water absorption as well as hormone signaling, which are closely involved in plant adaptation to its environment. Moreover, the interactions between the scion and the rootstock provides a broad range regarding adaptation strategies to different growing conditions and production aims. In vineyards, the most commonly rootstocks are hybrid breeds between American *Vitis* species (*V. berlandieri*, *V. riparia*, and *V. rupestris*) and sometimes *V. vinifera*. Despite recent findings revealing a large genetic diversity in these genetic backgrounds, rootstocks remain poorly studied, especially at the genetic level. The *V. berlandieri* hybrids have shown good performances in water deficit and limestone tolerance in vineyards.

A selection of 286 *V. berlandieri* genotypes were chosen from a field-grown population of plants obtained from seedlings at Hochschule Geisenheim University, Germany. The samples were analysed regarding their genetic structure, which revealed two subpopulations and an association between the climatic conditions of the sampling areas and their genetic variability. While an isolation by distance has been highlighted, it was not possible to detect the variability in the genetic burden of the two subpopulations.

This population was used for grafting of *V. vinifera* cv. Riesling (clone 24-209Gm), which was planted in pots and grown in the greenhouse for two consecutive years with no limiting conditions. A root phenotyping has been carried out after one year of growing, revealing a high variability at the phenotype and genetic level. The heritability was high for these traits which allowed to carry out a genome wide association study and to detect eleven genetic markers associated with root-related traits.

Each year, the population was planted in a field experiment in order to observe the variability of conferred traits induced by the rootstock to the scion. A medium to high variability has

been detected for the pruning weight and the $\delta^{13}\text{C}$ as well as a medium to high heritability. A genome wide association study has allowed us to detect two significant markers for $\delta^{13}\text{C}$ but no markers were highlighted for the pruning weight.

Correlations between root-related and scion conferred traits have been found. A comparison of the phenotypical performance of the *V. berlandieri* genotypes to commercial rootstocks, i.e. SO4, 110R, Börner and 5BB, resulted in interesting insights for the selection of future genotypes for rootstock breeding. This association study is the first carried out in a natural population of a wild *Vitis* monospecies and highlights new opportunities for grapevine rootstocks breeding.

German

Der Klimawandel erfordert die Anpassung von landwirtschaftlichen Produktionssystemen an die sich ändernden Umgebungsbedingungen. Strategien zur Anpassung können verbesserte Anbaumethoden oder die Auswahl des Pflanzmaterials sein. Bei veredelten Pflanzen, wie der Rebe, lassen sich verschiedene Edelreis \times Unterlagen-Kombinationen auswählen. Das Wurzelsystem der Pflanze ist verantwortlich für die Verbindung mit dem Boden, der Wasser- und Nährstoffaufnahme. Die Wahl der Unterlage ist ein wichtiges Anpassungsinstrument, mit dem sich viele physiologische Prozesse steuern lassen. Die im Weinbau am häufigsten verwendeten Unterlagsreben sind Hybriden zwischen amerikanischen *Vitis*-Arten (*V. berlandieri*, *V. riparia* und *V. rupestris*) und in seltenen Fällen auch *V. vinifera*. Trotz neuerer Erkenntnisse, die eine große genetische Vielfalt dieser genetischen Ressourcen offenbaren, sind die Unterlagsreben nach wie vor nur wenig erforscht. Dies gilt vor allem für die genetische Ebene.

Aus einer Sammlung von Sämlingen von wilden *V. berlandieri*-Populationen der Hochschule Geisenheim in Deutschland, wurden 286 Individuen ausgewählt und genotypisiert. Bei zwei Subpopulationen wurde ein Zusammenhang zwischen den klimatischen Bedingungen der Probenahmegebiete und der genetischen Variabilität festgestellt. Die räumliche Distanz konnte als ein Unterscheidungskriterium herausgestellt werden, jedoch konnte keine Variabilität in der genetischen Last der beiden Subpopulationen erkannt werden.

Die Wildreben wurden mit *V. vinifera* cv Riesling (Klon 24-209) veredelt und in zwei aufeinanderfolgenden Jahren als Topfreben im Gewächshaus kultiviert. Nach einem Jahr wurden eine Wurzelphänotypisierung durchgeführt. Es konnte eine hohe Variabilität auf phänotypischer und genetischer Ebene festgestellt werden. Die Heritabilität war bei den untersuchten Merkmalen hoch, so dass mittels einer genomweiten Assoziationsstudie elf genetische Marker ermittelt wurden, die mit wurzelbezogenen Merkmalen verbunden werden konnten.

Eine im Freiland gepflanzte Population wurde ebenfalls phänotypisiert und eine mittlere bis hohe Variabilität für das Schnittholzgewicht und $\delta^{13}\text{C}$ -Werten sowie eine mittlere bis hohe Heritabilität festgestellt. Eine genomweite Assoziationsstudie ermöglichte die Entdeckung von zwei signifikanten Markern für $\delta^{13}\text{C}$, aber es wurden keine Marker für das Schnittholzgewicht identifiziert.

Es wurden Korrelationen zwischen wurzelverwandten und vom Edelreis übertragenden Merkmalen festgestellt. Darüber hinaus ermöglichte ein Vergleich von kommerziellen Unterlagen (SO4, 110R, Börner und 5BB) mit der *V. berlandieri*-Population hinsichtlich der phänotypischen Leistungen der *V. berlandieri*-Genotypen die interessantesten Genotypen für zukünftige Unterlagskreuzungen hinsichtlich der untersuchten Parameter und Zielsetzungen herauszuarbeiten. Die vorliegende Assoziationsstudie ist die erste, die an einer natürlichen Population einer einzelnen Vitis-Wildspezies durchgeführt wurde und zeigt neue Möglichkeiten für die Züchtung von Unterlagsreben auf.

French

Dans le contexte du changement climatique, l'adaptation des plantes est d'intérêt majeur. L'adaptation peut être atteinte en modifiant les pratiques culturales, la gestion des parcelles ou le matériel végétal. Chez les plantes greffées, le matériel végétal peut être adapté en améliorant le greffon ou le porte-greffe. Parce que le porte-greffe est le système racinaire de la plante, il est responsable de l'ancrage et de l'absorption de l'eau et des nutriments qui sont étroitement impliqués dans l'adaptation des plantes. De plus, les interactions entre le greffon et le porte-greffe font du porte-greffe un levier pertinent pour l'adaptation. Au vignoble, les porte-greffes les plus utilisés sont des hybrides entre les espèces de *Vitis* Américains (*V.*

berlandieri, *V. riparia*, and *V. rupestris*) et parfois *Vitis vinifera*. Malgré des découvertes récentes révélant une importante diversité génétique au sein de ces fonds génétiques, les porte-greffes restent peu étudiés et encore moins au niveau génétique. Les hybrides de *V. berlandieri* ont montré de bonnes performances pour leur tolérance à la sécheresse et au calcaire dans les vignobles.

Grâce à la population naturelle de *V. berlandieri* collectée en 2005 et cultivée en champs à Geisenheim, Allemagne, 286 génotypes de *V. berlandieri* ont été échantillonnés et analysés pour leur structure génétique, révélant deux sous-populations et une association entre les conditions climatiques des aires de prélèvement et leur variabilité génétique. Une isolation par la distance a été révélée mais nous n'avons pas pu détecter de variabilité dans le fardeau génétique des sous-populations.

Cette population a été greffée avec Riesling (clone 24-209) sur deux années consécutives et cultivée en pots dans une serre en conditions non limitantes. Un phénotypage racinaire a été réalisé après un an de croissance, révélant une forte variabilité au niveau phénotypique et génétique. L'héritabilité de ces traits était forte et nous a permis de conduire une étude de génétique d'association et détecter 11 marqueurs génétiques associés aux traits liés aux racines.

Chaque année, la population a été plantée dans une expérimentation en champs dans le but d'observer la variabilité des traits conférés par le porte-greffe au greffon. Une héritabilité moyenne à forte a été détectée pour le poids des bois de taille et le $\delta^{13}\text{C}$. Une étude de génétique d'association nous a permis de détecter deux marqueurs significatifs pour le $\delta^{13}\text{C}$ mais aucun marqueur n'a été identifié pour le poids de bois de taille.

Des corrélations entre les traits liés aux racines et les traits conférés au greffon ont été trouvées. De plus, des porte-greffes commerciaux (SO4, 110R, Börner, and 5BB) ajoutés à la population de *V. berlandieri* nous ont permis de les comparer aux performances phénotypiques des génotypes de *V. berlandieri* pour l'ensemble des traits, mettant en évidence quelques génotypes intéressants pour la sélection. Cette étude de génétique d'association est la première conduite sur une population naturelle d'espèce unique de porte-greffes de vigne et elle a permis de dégager de nouvelles opportunités pour l'amélioration des porte-greffes.

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List of abbreviations

ABA: Abscisic Acid

AGAP: Amelioration Genetique et adaptation des Plantes méditerranéennes et tropicales

AIA: Auxin

Av_Diam: Average Diameter

BAG: Bordeaux Adelaide Geisenheim

BIC: Best Indicator Criteria

BLINK: Bayesian information and Linkage Disequilibrium Iteratively Nested Keyway

BLUE: Best Linear Unbiased Estimate

BLUP: Best Linear Unbiased Predictor

C: Carbon

CI: Cool night Index

CIRAD: Centre de cooperation Internationale en Recherche Agronomique pour le Developpment

CNIV: Comité National des Interprofessions des Vins à appellation d'origine et à indication géographique

CO₂: Carbon dioxide

CV: Coefficient of Variation

DI: Dryness Index

DNA: Deoxyribonucleic Acid

EGFV: Ecophysiologie et Genomique Fonctionnelle de la Vigne

F1: Progeny of First generation

FarmCPU: Fixed and random model Circulating Probability Unification

FEM: Finite Element Method

GA: Gibberellin

GATK: Genome Analysis Toolkit

GBS: Genotyping By Sequencing

GEA: Genome-Environment Association

GLM: Generalized Linear Model

GS: Genomic Selection

GST: Growing Season Temperature

GSR: Growing Season Rainfall

GWAS: Genome Wide Association Study

H²: Broad sense heritability

HI: Huglin Index

HST: Heat Stress index

HYB: Branas Hydrothermal index

HWE: Hardy-Weinberg Equilibrium

IBD: Isolation By Distance

INRAE: Institut National de la Recherche pour l'Agriculture, l'Alimentation et l'Environnement

ISVV: Institut des Sciences de la Vigne et du Vin

LD: Linkage Disequilibrium

MAS: Marker Assisted Selection

MCMC: Monte-Carlo Markov Chain

MLM: Mixed Linear Model

N: Nitrogen

NB_Large: Number of Large roots

NB_Medium: Number of Medium roots

NB_Small: Number of Small roots

NCBI: National Center for Biotechnology Information

NILs : Near Isogenic Lines

OIV : Organisation Internationale de la Vigne et du Vin

P : Phosphorus

P_{del} : Proportion of deleterious variants

PC : Principal Component

PCA : Principal Component Analysis

Prop_Large : Proportion of Large roots

Prop_Medium : Proportion of Medium roots

Prop_Small : Proportion of Small roots

PW : Pruning Weight

QC : Quiescent Center

QQ : Quantile-Quantile

QTL: Quantitative Trait Loci

QTN: Quantitative Trait Nucleotide

RD: Roger's Distance

RDW: Root Dry Weight

REM: Random Effect Model

REML: Restricted Maximum Likelihood

RFLP: Restricted Fragment Length Polymorphism

RGB: Red Green Blue

RILs: Recombinant Inbred Lines

RRSPR: Springtime Rainfall

SCD: Steep Cheap and Deep

SFR: Spring Frost Risk

SNP: Single Nucleotide Polymorphism

SSR: Single Sequence Repeat

TMV: Tobacco Mosaic Virus

Tot_Diam: Total Diameter

UMR: Unité Mixte de Recherche

UPGMA: Unweighted-Pair-Group with Arithmetic Mean

USA: Unated States of America

VCF: Variant Calling File

WFR: Winter Freeze Risk index

WUE: Water Use Efficiency

$\Delta^{13}\text{C}$: Isotopic carbon discrimination

ψ_{pd} : Pre-dawn water potential

General Introduction

The major importance of plants on earth is well known, they produce oxygen, human and animal food, a lot of different molecules with miscellaneous usages and they fix carbon thanks to the light energy. They can also be materials and energy resources. Therefore, the interests and goals of plant domestication and breeding are clear: improve yield to feed the increasing population, produce materials and molecules for human development, adapt fast to the changing environment, absorb CO₂ and limit fertilization and pesticides usage in field. Hopefully, most of the traits involved in these interests and goals are controlled genetically by one or, most of the time, several genes interacting with environmental conditions (Paterson et al. 1988). The genetic information can be accessed by sequencing. During the last few years, the improvement of sequencing techniques made it easier and cheaper to access genetic information. Genetic studies started with the detection of the genetic origin of human diseases and nowadays genetics is a common tool in research on human health, animal and plant breeding. Moreover, because it is easier to duplicate and cross plants, several generations can be obtained in few years. It makes it possible to improve a cultivar in few years with plant breeding. In perennial plants, more time is needed because of the long development cycle and the higher complexity to carry out quantitative genetics studies.

In the world, grapevine is cultivated mainly for producing wine (261,737,000 hl produced in 2021; OIV) or table grapes (30,107,366 tons produced in 2021, OIV). The world's vineyard surface area was 7,327,311 ha in 2021. The largest wine producer is Italy (50,232,000 hl), France (37,648,000 hl) is the second, and Germany is 9th (8,744,000 hl). In France, vineyard surface area represents 3% of the cultivated area but wine represents 15% of the agricultural production in term of value (CNIV accessed in 2022).

In the climate change context, it is of major interest to adapt crops. Since the phylloxera crisis, grapevine is cultivated grafted with hybrids between American *Vitis* species (*V. rupestris*, *V. riparia*, and *V. berlandieri* the most popular) as rootstocks. Several ways are available to adapt grapevine by changing cultural practices (plant density in field, shoot pruning, watering the field...) or by acting on the plant material (van Leeuwen and Destrac-Irvine 2017; van Leeuwen

et al. 2019). The plant material can be adapted by planting other varieties more adapted to a region, leading to modifications in wine typicity. In addition, the clonal variability makes it possible to be better adapted; however, clonal selection contribution is limited because of the low genetic variation that exist between clones. The other option is to adapt grapevine by selecting rootstocks. Since the rootstock is the root system of the plant managing water and nutrient absorption and the interactions that occur between the scion and the rootstocks, it represent a very good driver of grapevine adaptation (Ollat et al. 2016). However, while the genetic diversity of American *Vitis* species has been highlighted (Péros et al. 2021), studies on rootstock genetics and root traits remain scarce (Marguerit et al. 2012; Bert et al. 2013; Tandonnet et al. 2018; Alahakoon and Fennell 2023).

In this context, the aim of the PhD project presented below is to explore the genetic diversity of *V. berlandieri*, a well-known American *Vitis* genetic background used in the most used hybrids commercial rootstocks. The root-related traits variability will be analyzed in the population in order to identify correlations between the young root system profile and traits conferred to the scion (vigor and water use efficiency) in a grafted field experiment. The genetic determinism of root-related traits and trait conferred to the scion will be explored in order to highlight genetic regions associated with these traits. At the end of this work, we plan to select the most interesting genotypes of the population and few genetic markers that can be used in grapevine rootstocks breeding programs.

This PhD project has been realized in a cotutelle program between Bordeaux, France and Geisenheim, Germany. The cotutelle program depends on the Bordeaux, Geisenheim, and Adelaide (BAG) alliance. The fundings went from the Région Nouvelle Aquitaine (France) and the Land Hessen (Germany). In France, the work has been realized in UMR n°1287 EGFV (Ecophysiologie et Génomique Fonctionnelle de la Vigne), the University of Bordeaux and the SVS (Science de la Vie et la Santé) doctoral school. In Germany, the work has been done in the Hochschule Geisenheim University and the Department of Grapevine Breeding. During the PhD project, the time spent in the two partners was evenly distributed (18 months in each country). A part of the results was presented with an oral communication to the Grapevine Breeding and Genetics Congress, July 2022, in Germany. Several collaborations occurred during the project for the *V. berlandieri* population libraries preparation that was made with genotyping platform of the UMR AGAP (Amélioration Génétique et Adaptation des Plantes

méditerranéennes et tropicales) in Montpellier, France and the sequencing was made with the GENEWIZ company. Vincent Segura from UMR AGAP and Marie Béatrice Bogeat Triboulot from UMR EEF also supported the PhD project process by giving technical and scientific advice. The PhD project is related with the French national program of grapevine rootstock genetic improvement, managed by INRAE. This program presents two strategies: first, creating new varieties and secondly, characterizing existing rootstocks for potential use in the French vineyard. Thus, the PhD project allows us to dissect the genetic architecture using another approach than QTLs detection within a pedigree population.

This manuscript is divided into seven chapters:

The **first chapter** introduces the scientific context of the project about the interest of genetic studies for plant breeding, the knowledge on plant root systems, their potential in crop adaptation, and the impact of root-related traits on the vegetative part of the plant, more precisely in the grafted context.

The **second chapter** describes the materials and methods used during the PhD project.

The **third chapter** presents, as a paper submitted to Evolutionary Applications, the genetic structure of the population of *V. berlandieri* and exploration of the association between the genetic and the environmental variability.

The **fourth chapter** describes, as a paper submitted to Theoretical Applied Genetics journal, the root-related traits phenotypic variability in the population of *V. berlandieri* and its association with the genetic variability in order to highlight genetic markers associated with these traits.

The **fifth chapter** considers the part of the scion phenotypic variability due to the *V. berlandieri* rootstocks for vigor and water use efficiency.

The **sixth chapter** contains the general discussion and my perspectives.

The **seventh chapter** is the overall conclusion

Chapter 1: Scientific context

"Knowledge is power"

Sir Francis Bacon

1.1 From the genetic perspective

1.1.1 Plant breeding tools

1.1.1.1 *Quantitative genetics and association mapping*

Progress in plant breeding has been made for a long time through mass selection, the goal being to select the more performant individuals in a population for traits of interest. Then, these individuals are crossed together in order to obtain progeny and to select genotypes that perform better than the two parents. Current genetic tools allow deeper deeper analysis and ability to detect genetic regions involved in the phenotypic variability. Two main approaches are used, the **quantitative** genetic studies to detect quantitative trait loci (QTL) are based on the occurrence of recombination events in a progeny (Tanksley 1993), and **genome wide association studies** (GWAS) based on linkage disequilibrium and allele frequency in a population (R. J. Klein et al. 2005) which also allow to detect QTL. The **genomic selection** model, based on pedigree and markers information to predict performances in progeny (Meuwissen, Hayes, and Goddard 2001), are also used in breeding but won't be developed here.

In genetic studies, one variable **quantitative** trait is explored in **progeny** or **population**. To do so, the trait **phenotype** is quantified for simple traits like height, weight, number of fruits, etc. or more complex traits such as sap flow, anatomical insights and more. The phenotype **variability** can be partitioned into two elements: the part of the variability due to environment and the part of the variability due to the genetics. In a genetic study context, it is of major interest to consider the genetic part of the **variability**, also called the **broad sense heritability** (H^2), because the efficiency of selection depends on the portion of the phenotypic variability due to the plant genetics (Fehr 1987).

To carry out a quantitative genetic study, two individuals differing in their performances for a quantitative trait of interest are needed. Then, markers distinguishing the genotype of these individuals are required (see next section). The two individuals are crossed together to obtain a population in which the **variability** of the trait of interest is expected to be high. The molecular markers will segregate with the trait value allowing a statistical detection of it. The size of this signal depends on the intensity of the correlation between the genetic variability and the trait values. The extent of the signal depends mainly on the number of **recombinations** in the genetic region of the marker. If no recombination event occurs in the genetic region containing a gene of interest, it won't be possible to detect it. Thus the

population size is of major importance to be able to detect loci involved in the phenotypic variability (Cockram and Mackay 2018).

GWAS studies use the **linkage disequilibrium** (LD) non-random association between markers to detect links with phenotypic variation. Modification in **allelic frequency** is the results of years of recombination after crossings (Nordborg and Tavaré 2002). Moreover, no mapping population is needed which makes it simpler and faster to carry out. The main limitation in using GWAS is the higher potential of detecting **false positive** and **false negative** signals. Many events can affect the LD variation across population genome which can lead to the detection of markers which are not physically linked to the genetic region involved in the trait determinism (Thornsberry et al. 2001) leading to false positive results. Population **structure** and individual's relationships are the most important sources of interference, leading to the detection of false positive in a lot of studies (Kang et al. 2010; 2008; Zhang et al. 2010). Then, a lot of efforts were made to avoid false positive detection, mainly by distinguishing **subpopulations** in the main population.

Different models were developed to first reduce false positive detection and then to reduce the calculation time. Population structure has been corrected with **generalized linear model** (GLM) using this parameter as **fixed effect**. The population structure can be incorporated as a proportion of the individuals belonging to each subpopulation (Pritchard, Stephens, and Donnelly 2000; Pritchard et al. 2000) or as PCA (principal component analysis) results. Relationships among individuals can be detected by including all markers as random effects; these markers can detect the variance of quantitative trait nucleotides (QTNs) according to linkage disequilibrium. Another way to detect kinship is to use all markers to obtain a kinship matrix among individuals. This matrix is then used as random effect. Both can be included in **mixed linear model** (MLM) as random and fixed effect but the calculation time was extremely long. Later different models were created to reduce the calculation time without improving statistical power. Recently, the statistical power has been improved with two new methods:

1) **FarmCPU** (Liu et al. 2016) is a method developed to improve statistical power in GWAS. This method divides the genome in several bins of equal size, then one marker with the lowest p-value is kept as pseudo QTN for each bin by random effect model. At the end, all pseudo-QTN selected are sorted by p-value and two models are used (FEM and REM) to select

best pseudo-QTNs. The main limitation in this method is the assumption of regular distribution of QTNs across the genome which is almost never the case.

2) In **BLINK** (Bayesian information and Linkage disequilibrium Iteratively Nested Keyway; Huang et al. 2018) method, bins are replaced by the linkage disequilibrium information. This method has shown better performances than others in significant markers detection, with a lower computing time (three times faster than FarmCPU on R) (Huang et al. 2018). In this model, bins are replaced by **LD information** in the QTN detection step. Moreover, the genetic to residual variance ratio is optimized by substituting REML with BIC, which directly solves residual variance without iteration. These two modifications improved computing time and reduced false positive and negative detection in GWAS (Huang et al. 2018).

1.1.1.2 Genetic resources and molecular markers

After 1980, the improvement of molecular biology technics allowed the use of two new genetic markers: Restriction Fragment Length Polymorphism (RFLP) (Beckmann and Soller 1983) and microsatellites (Single Sequence Repeat, SSR). These markers allowed capturing the polymorphism in DNA sequences and then carrying out QTL and GWAS in crop plants (Mohan et al. 1997). Nowadays, **single nucleotide polymorphism** (SNPs) are markers of choice for their convenience in data management. Moreover, their number and their polymorphism are high in the genome, and with sufficient density (when the number of markers per Kb is close to the distance of linkage disequilibrium decay); therefore, SNPs allow a fine exploration of genome variability.

The fast evolution of sequencing technologies are due to the Human Genome Project (International Human Genome Sequencing Consortium 2004) which has allowed at the same time to see the appearance of the first whole genome sequencing of reference species (bacteria, yeast, plant) including *Arabidopsis thaliana* (The Arabidopsis Genome Initiative 2000). The first plant whole genome sequencing was obtained at the end of the 20th century with the *Arabidopsis thaliana* (The Arabidopsis Genome Initiative 2000). This plant was chosen as model plant because the genome size is relatively short (130 Mb) and the life cycle (2 month) which allows several generations to be obtained in a year with a lot of individuals (around 2 000). Moreover, this plant has no economic interest which has facilitated results

sharing between countries. Later on, the rice genome was published (Sasaki 2005), and a lot were following including the first reference genome of grapevine and 4th higher plant (*Vitis vinifera*, “PN20024”) an inbred genotype of the well known Pinot noir variety published in 2007 (Jaillon et al. 2007; Velasco et al. 2007).

1.1.2 Targets and uses of QTL in breeding

1.1.2.1 From QTL to marker assisted selection

The availability of reference genomes make it easier to carry out quantitative genetic and association mapping studies to detect QTL. According to the LD, DNA quality, number of markers, population size and model used, the genetic region detected can have various sizes and include a wide range of number of genes. Therefore, further studies are needed after the detection of a QTL to identify which gene or group of genes is involved in the variability of the studied trait (Figure 1.1). It can be done through genetic engineering (e.g. knock out or mutant tests), creating RILs (recombinant inbred lines) or NILs (near-isogenic lines) population. In breeding, QTL are widely used to improve plant performance. After detection and validation, QTL can be used in **marker assisted selection** (MAS) (Tuberosa et al. 2007). The goal is to transfer the QTL in a new “elite variety”. This technique presents an advantage at short and medium time frame compared to classical phenotypic selection focusing on the transfer of QTL with high effect (Hospital and Charcosset 1997).

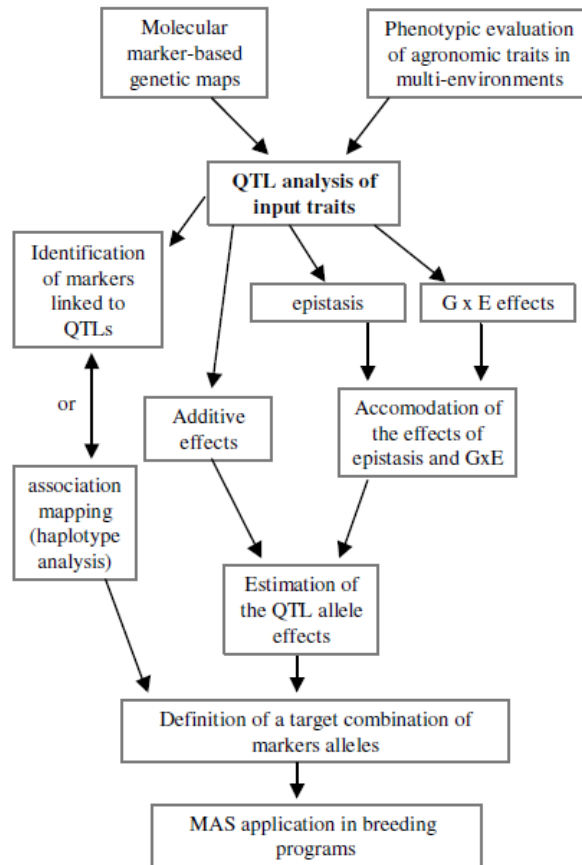


Figure 1.1 : Marker assisted selection workflow (Francia et al., 2005)

The use of QTL studies and MAS in breeding are simpler than phenotypic screening because selection can be done at seedling stage and homozygous/heterozygous plants can be detected and then one plant of interest can be directly selected (Collard and Mackill 2008). MAS allows tracing favorable alleles across generations, selecting the best individuals precisely and go beyond the linkage between a gene of interest and unfavorable loci due to LD (Francia et al. 2005). It can be used to reduce population size for back-crossing by selecting good donors, to select more complex traits and transfer recessive genes. Knapp (1998) estimated that phenotypic breeding needs 1.0 to 16.7 times more individuals in a population to have a chance to select one superior genotype in comparison with MAS breeding. However, the full exploitation of MAS potential was considered as not reached in 2008 and yet remaining a strategic tool for breeding (Collard and Mackill 2008). MAS led to rice improvement (Das, Patra, and Baek 2017) and tomato resistance against the tobacco mosaic virus (TMV)(Young and Tanksley 1989). Because of the extended generation time of perennials (Neale and Kremer 2011), the use of MAS represents a strong interest. The method has been applied on sugi for

male sterility (Moriguchi et al. 2020), on fruit trees for gametophytic self-incompatibility (Yamane and Tao 2009; Tao and Iezzoni 2010), and on *Vitis* for powdery and downy mildew resistance (Eibach et al. 2007).

Moreover, similarities exist between genomes (orthology and synteny) and the marker order is highly conserved across related species (Paterson et al. 2000; 2009; Zou et al. 2020) which allows to use QTL information from a species to focus on a specific region for QTL detection in another related one.

1.1.2.2 *Quantitative genetics*

QTL were first identified in *Arabidopsis thaliana* for flowering time (Alonso-Blanco et al. 1998; Clarke et al. 1995; Kowalski et al. 1994). Then, *Arabidopsis* was used in a lot of QTL studies (Koornneef, Alonso-Blanco, and Vreugdenhil 2004). These findings led the private sector to invest in the development genomic tools for other plants like maize, soybean, canola, cotton and sunflower (Xu and Crouch 2008), leading to improved commercial breeding programs.

In crops, QTL studies focused on three main domains, the increase of **yield** and **quality**, **biotic** and **abiotic** stress tolerances. QTL helped improve yield in maize, rice, barley and soybean (Francia et al. 2005). QTL and MAS have been used to improve bread making and pasta quality in wheat (Dubcovsky 2004). In cereal crops, a lot of QTL studies focused on biotic stress like resistance against cyst nematode (Eastwood et al. 1991; Eagles et al. 2001) or root lesion nematode (Zwart, Thompson, and Godwin 2004) in wheat. QTL can be used to transfer biotic tolerance to a variety by **pyramiding** several genetic regions that confer tolerance. The goal of pyramiding is to accumulate tolerance sources to avoid a quick bypassing of the tolerance. It has been done in barley for rust resistance (Castro et al. 2003), yellow mosaic virus (Okada et al. 2004; Werner, Friedt, and Ordon 2005), in rice for bacterial blight (N. Huang et al. 1997; Datta et al. 2002), blast disease (Hittalmani et al. 2000) or in wheat for powdery mildew (Liu et al. 2000). Pyramiding QTL in the elite varieties by backcrossing makes the MAS even more efficient in breeding programs (Hospital and Charcosset 1997). A wide range of abiotic stress have been subjected to QTL studies, like low temperature stress tolerance, drought stress, salinity and aluminium as well as quality traits in tomato, malting barley, wheat, cotton and rice (Francia et al. 2005). Indeed, QTL for drought tolerance have been identified in wheat

(Merchuk-Ovnat et al. 2016) and in chickpea (Hamwiah, Imtiaz, and Malhotra 2013), for salt tolerance in soybean (Ha et al. 2013) or frost in pea (Klein et al. 2014). Pyramiding has been applied in rice for QTL involved in drought stress, salinity and submergence (Muthu et al. 2020) and for drought and salt tolerance in maize (Nguyen et al. 2013).

Intensive agronomic crops were the subject of the first QTL analyses mainly for their economic interest. However, it is clear that the use of QTL and MAS in perennial crops is also of major interest. Perennial plants are mainly trees whose genome size vary widely across species from 265 Mb (*P. persica*) to 31 Gb (*P. lambertiana*) (Neale et al. 2017). Genetic studies on trees remain scarce mainly because of limitations due to their long life cycle (Khan and Korban 2012), the space needed for growing them and their genome size (González-Martínez et al. 2007).

Trees can be cultivated for wood or for fruits, which implies different breeding targets. In trees cultivated for wood, a few quantitative genetic studies are available on maritime pine for height growth and stem straightness (Bartholomé et al. 2016) or $\delta^{13}\text{C}$ (Brendel et al. 2002). In fruit trees, breeding focuses mainly on biotic and abiotic stress resistance, yield, and fruit quality. One of the best illustrations of the interest of using quantitative genetic on trees is the FruitBreedomics project (2011-2015). This project was initiated to improve breeding opportunities on apple and peach in Europe. The objectives were to develop new tools and softwares, identify genetic targets involved in the determinism of agronomic traits and develop plant material and tools for breeders. Laurens et al. (2018) reviewed the results of this project and highlighted its benefits for apple and peach crops. Genetics studies carried out during this project allowed detecting QTL for several traits. 2 loci were identified for slow melting flesh trait in peach with 20% of phenotypic variation explained by each. Markers associated with brown rot resistance in peach were identified in F1 progeny (Pacheco et al. 2014).

In QTL mapping studies, because results depend on recombination events in a specific meiotic event, QTL detected for a specific progeny remain uncertain for the entire species. To overcome this issue, **meta-QTL analysis** are useful tools for compilation of QTL information from several F1 progenies allowing the validation of constant QTL (Veyrieras, Goffinet, and Charcosset 2007). Abdelraheem et al. (2017) identified 28 QTL clusters on 15 chromosomes

for abiotic and biotic resistance in tetraploid cotton. These hotspots can then be used in MAS. Other metaQTL analyses has allowed the detection of QTL involved in yield in maize (Yijun Wang et al. 2020), drought tolerance in wheat (Kumar et al. 2020), seed iron and zinc concentration in bean (Izquierdo et al. 2018), fusarium resistance in wheat (Liu et al. 2009) or blast resistance in rice (Ballini et al. 2008). Meta-QTL analysis has been carried out on perennials for plum pox virus resistance in apricot tree (Marandel et al. 2009), for fruit quality trait in apple tree (Costa 2014) and for disease resistance traits in *Theobroma cacao* (Lanaud et al. 2009).

1.1.2.3 Association mapping

In plants, the first **association mapping** study was carried out in maize for flowering time (Thornsberry et al. 2001). They adapted the genetic association mapping method from human health studies considering the maize genetic structure to control false discovery rate, reducing it by up to 4.7 fold. Then, GWAS led to successful application of detection of QTL involved in the determinism of flowering time in *Arabidopsis thaliana* (Olsen et al. 2004). Zhao et al. (2011) detected QTL with GWAS for 413 accessions of rice for 34 traits. In maize, Kump et al. (2011) identified 32 QTL intervals for resistance to southern leaf blight, Tian et al. (2011) identified 30-36 QTL for three leaf trait and Li et al. (2013) showed that 83% of the phenotypic variation of oil concentration can be explained by 26 loci in maize kernel.

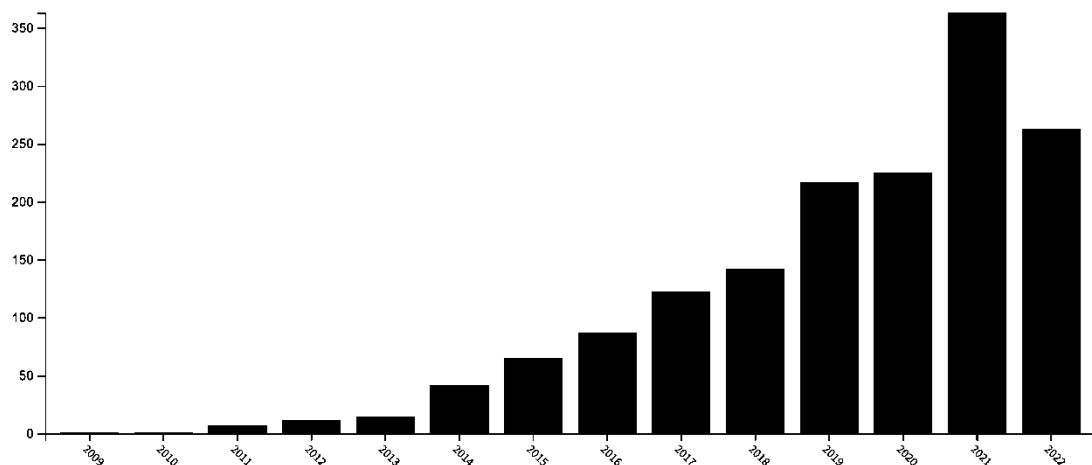


Figure 1.2: Number of publications obtained from Web of Science for: "GWAS AND Plant" research equation (obtained the 10/24/2022).

GWAS is better suited for QTL detection than quantitative genetic studies in trees because the creation of a segregating population is not needed (Khan and Korban 2012). GWAS is thus preferred for QTL detection in trees. Moreover, the cost of sequencing is decreasing rapidly, the accuracy of GWAS models is getting better and there is a need of going faster in breeding programs in plants. Thus, the number of GWAS studies has been increasing recently (Figure 1.2).

One limitation for using GWAS for trees is the cost and the time of phenotyping. However, high speed methods have been used recently, in Mediterranean Pine, Santini et al. (2021) developed a semi-automatic phenotyping workflow reducing the cost and the time needed for trees phenotyping. The phenotyping was based on red, blue, green (RGB), multispectral and thermal images acquisition. They identified 12 SNP related to growth traits each explaining between 5% and 10% of the total phenotypic variation, 6 SNP related to transpiration and leaf water content (4%-5% variation explained) and 11 SNP related with leaf pigments and leaf area (3%-5% variation explained).

GWAS are carried out on woody species according to their use (fruit or wood). Conifers are mainly cultivated for wood; therefore, breeding focuses on growth characteristics like volume, height and ring width. Loci of interest were detected with GWAS for growth in *Populus tomentosa* (Tian et al. 2012; Du et al. 2014; Xu et al. 2014; Du et al. 2015; Yang et al. 2016), *Picea glauca* (Lamara et al. 2016), *Picea miriana* (Prunier et al. 2013), *Pinus pinaster* (Bartholomé et al. 2016), *Pinus radiata* (Dillon et al. 2010), *Populus tremula* (Ma et al. 2010), and *Pinus taeda* (Cumbie et al. 2011). The second principal target in conifer breeding is the wood quality which corresponds to the density, the composition, and fiber properties of wood. These traits are more expensive and time consuming to be measured than growth parameters. In GWAS studies, loci of interest for these traits have also been highlighted in *Populus tomentosa* (Tian et al. 2012; Du et al. 2013; 2014; Tian et al. 2014; Wang and Zhang 2014; B. Xu et al. 2014; Du et al. 2015; Chen et al. 2016; Yang et al. 2016), *Pinus taeda* (González-Martínez et al. 2007; De La Torre et al. 2019), *Pinus radiata* (Dillon et al. 2010), *Pinus pinaster* (Lepoittevin et al. 2012), *Corymbia citriodora* (Dillon et al. 2012), *Populus nigra* (Guerra et al. 2013), *Populus trichocarpa* (Wegrzyn et al. 2010; Porth et al. 2013; McKown et al. 2014), *Eucalyptus nitens* (Southerton et al. 2010), *Eucllyptus globulus* (Thavamanikumar et

al. 2014), *Eucalyptus pilularis* (Sexton et al. 2012), *Picea glauca* (Lamara et al. 2016) and *Cryptomeria japonica* (Uchiyama et al. 2013).

De La Torre et al. (2022) studied coast redwood and giant sequoia for 10 drought related traits highlighting 78 markers associated with drought in coast redwood and 6 in giant sequoia. GWAS have also been used to detect markers involved in callus differentiation in *Populus euphratica* (Zhang et al., 2020).

In fruit trees, 7 genomic regions involved in the genetic determinism of fruit quality traits in citrus have been highlighted (Imai et al. 2018). Mariette et al. (2016) detected an already known loci of resistance for *Plum Pox Virus* tolerance in apricot as well as new potential loci of interest thanks to association genetics. GWAS for peach for fruit quality (Micheletti et al. 2015) identified several loci for acidity, fruit fresh color, fruit pubescence, fruit shape and texture. In *Prunus*, (Tan et al. 2021) used 5 species (peach, plum, apricot and 2 wild peach species) genetic structural variants to carry out a GWAS that identified 11 qualitative and 8 quantitative traits. Structural variations were associated with fruit shape, fruit development timing and double-flowering phenotype. In apple, GWAS was used to detect genetic regions involved in flowering and ripening period (Urrestarazu et al. 2017) and 5 loci were identified associated with apple blotch disease (Noh et al. 2020). In pear, after 3 years of phenotyping, 37 loci were associated with 8 fruit quality traits (single fruit weight, stone cell content, fruit skin color, coverage ratio of fruit russet, location of fruit russet, furrows on fruit surface, direction of carpodium and direction of sepal) and 3 with the phenology of the plant (initial bloom period days if fruit development and days of vegetative growth (Zhang et al. 2021). It promoted the identification of a candidate gene *PbrSTONE*, functionally validated for the regulation of stone cell formation which is of major interest in fruit quality. Minamikawa et al. (2018) also used the combination of a pear parental population and a breeding population to increase the power of GWAS and GS to characterize 18 fruit quality traits. The same method also increased the resolution of GWAS results in citrus for characterizing 17 fruit quality traits (Minamikawa et al. 2017). They suggested a potential higher efficiency of MAS in breeding thanks to the increased the accuracy of their models.

GWAS has been rarely carried out in grafted perennial plants. In grafted plants either the scion genotype or the rootstock genotype can vary in the population. Otherwise, it makes it

impossible to assign the origin of phenotypic variations. However, recently GWAS was conducted on 241 cultivars of apple tree grafted to the same rootstock by Coupel-Ledru et al. (2022) for tree architecture, light interception and water-use related traits.

1.1.3 Genetic in grapevine

Historically, grapevine has been improved by mass selection. Hybrids have been obtained by crossing cultivated grapevine (*Vitis vinifera subsp. vinifera*) or cultivated grapevine with wild individuals (*Vitis vinifera subsp. sylvestris*). It is estimated that almost 10,000 varieties exist around the world (This, Lacombe, and Thomas 2006).

Cultivated *Vitis vinifera* is clonally propagated which allows maintaining genetic diversity but limits mixing through recombination events during crossings. It has been suggested that **clonal propagation** leads to bottleneck and to the accumulation of deleterious variants in crops but the impact of domestication (5.2% more deleterious variants in cultivated grape) did not decrease fitness (Zhou et al. 2017).

The total grapevine **genome size** is around 500 Mb for 19 linkage groups (Jaillon et al. 2007; Velasco et al. 2007). 26 whole genomes are available for grapevine on NCBI (Sayers et al. 2022) for *Vitis vinifera*, American *Vitis* and hybrids. The genetic diversity explored in European germplasm revealed genetic structure stratification (Emanuelli et al. 2013) which has to be considered in genetic studies. Genetic quantitative studies on grapevine are carried out on different traits according to the above or below part of the plant. For scion, quantitative genetic focuses mainly on **disease resistance** (Fischer et al. 2004; Hoffmann et al. 2008; Riaz et al. 2011; Feechan et al. 2013; Rex et al. 2014; van Heerden et al. 2014; Ochssner, Hausmann, and Toepfer 2016; Zyprian et al. 2016) on **yield** (Doligez et al. 2002; Doligez et al. 2010; Marguerit et al. 2009; Fanizza et al. 2005; Costantini et al. 2008) and **quality of grapes** (Battilana et al. 2009; Costantini et al. 2008; Doligez et al. 2002; Fischer et al. 2004; Fournier-Level et al. 2009; Guillaumie et al. 2013), **phenology** (Costantini et al. 2008; Fischer et al. 2004; Marguerit et al. 2009; Zyprian et al. 2016) and **abiotic stress tolerance** (Bert et al. 2013; Marguerit et al. 2012). Most of quantitative studies are carried out on the scion part because rootstocks, being the root system of the plant, are more complex to study. While rootstocks can be used to improve performance of the scion through its interactions with the vegetative

part (Ollat et al. 2016), rootstocks genetic remains slightly explored and QTL studies on root-related traits remain scarce (Tandonnet et al. 2018).

A few GWAS studies can be found on grapevine on *Vitis vinifera* (Myles et al. 2011; Migicovsky et al. 2017; Laucou et al. 2018; Marrano et al. 2018; LaPlante et al. 2021; Flutre et al. 2022) or more recently on *Vitis spp.* (Yang et al. 2017; Zhang et al. 2017; Liang et al. 2019; LaPlante et al. 2021; Trenti et al. 2021; Wang et al. 2021) but except *V. vinifera*, no other grape genetic background has been explored yet (Table 1.1). Moreover, most of these studies are done on plant coming from **germplasms** (Table 1.1).

Table 1.1 : GWAS studies on grapevine (SNP= single nucleotide polymorphism, GBS = genotyping by sequencing)

Authors	Year	N	Population	Trait	N markers	Plants origin
Fournier-Level et al.	2009	141	<i>Vitis vinifera</i>	Anthocyanin	20 SSR and 129 SNP	Germplasm collection from INRA (Vassal, Hérault, France)
Emanuelli et al.	2010	148	<i>Vitis vinifera</i>	Aromas	95 SNP	Germplasm collection from INRA (Vassal, Hérault, France)
Myles et al.	2011	289	<i>Vitis vinifera</i>	Grape color	5387 SNP (Vitis9KSNP array)	USDA grape germplasm (Davis, California and Geneva, New York)
Migicovsky et al.	2017	580	<i>Vitis vinifera</i>	Flower sex, Skin color, Muscat aroma, Berry size	6,114 SNP (Vitis9KSNP array)	USDA grape germplasm (Davis, California and Geneva, New York)
Yang et al.	2017	96	<i>Vitis spp.</i>	Aromas	187 SSR	Collection of Shenyang Agriculture University (Liaoning Province, China)
Zhang et al.	2017	199	<i>Vitis spp.</i>	Seedlessness	414,223 SNP (GBS)	National Grape Germplasm Repository at Zhengzhou (China)
Laucou et al.	2018	783	<i>Vitis vinifera</i>	Sex, berry color, seeds, flavor, phenology, fertility, cluster and berry weight	10,207 SNP (18k SNP genotyping array)	4 grapevine collections in France, Spain (x2) and Germany
Marrano et al.	2018	92	<i>Vitis vinifera</i> subsp. <i>Sylvestris</i> and <i>sativa</i>	6 domestication related traits	26,893 SNP (Vitis20K SNP array and RAD-seq approach)	FEM grape germplasm (San Michele all'Adige, Italy)
Guo et al.	2019	179	<i>Vitis spp.</i>	Berry related traits	32,311 SNP (GBS)	National Grape Germplasm Repository at Zhengzhou (China)
Liang et al.	2019	185/222/334	<i>Vitis spp.</i>	Aromas/Berry content and Panicle type/Berry shape, color, weight, seed and Brix	8,734,701 SNP/ 9,068,232 SNP/ 9,191,395 SNP (resequencing)	Vitis germplasm (Beijing, China) National Grape Germplasm Repository at Zhengzhou (China)
Wang et al.	2021	119	<i>Vitis spp.</i>	Cold tolerance	1.04 million SNP from whole genome sequencing	Wild grapes collected in the Jilin province in China maintained in IBCAS (Beijing, China)
LaPlante et al.	2021	399	<i>Vitis vinifera</i>	5 mite recruitment related traits	4523 SNP (Vitis 9k SNP array)	USDA Grape Germplasm (Wolfskill Farms in Winters, Canada)
Trenti et al.	2021	100	<i>Vitis spp.</i>	Stomatal conductance and water stress	16,562 SNP (GrapeReSeq 20K SNPs array)	Germplasm of the University of Milan (Italy)
Flutre et al.	2022	279	<i>Vitis vinifera</i>	Berry related traits Vegetative growth Water relation ($\delta^{13}C$)	Around 14,000 SNP (GrapeReSeq 18k Vitis microarray) and 184,145 SNP (GBS)	Germplasm collection from INRA (Vassal, Hérault, France)

The first GWAS on *Vitis* was conducted by Fournier-Level et al. (2009) on the genetic architecture of anthocyanins content in berry skins. Five genetic regions (MYB proteins) were associated with the berry color explaining 84% of the phenotypic variation. Myles et al. in 2011 used the *Vitis9KSNP* array to access the genetic information on 5 110 SNPs from 289 *V. vinifera* accessions (table and wine grapes). They used berry color as a phenotypic trait and mixed

model implemented in EMMA with IBS matrix from PLINK as random effect to conduct a GWAS and detect signatures of selection. They found a signal on chromosome 2 (5Mb region) including a group of MYB transcription factor genes known to be involved in the grape color determinism. The rapid LD decay and the low number of SNPs didn't allow them to detect a narrower genetic region. Then, the rapid LD decrease has been confirmed in successive GWAS studies (Migicovsky et al. 2017; X. Yang et al. 2017; Laucou et al. 2018; Flutre et al. 2022). LD is a very important indicator in plant genetics (Remington et al. 2001) and even more so in GWAS. It allows selection of a high number of markers to be able to capture the genetic variability in a population and then detect significant association between traits and genetic regions. However, the number of markers used varied widely from 5110 (Myles et al. 2011) to 9M (Liang et al. 2019). The method of sequencing has a strong impact on the number of SNP detected, arrays allow only the detection of a small number of SNP around 10 000 (Myles et al. 2011; Migicovsky et al. 2017; Laucou et al. 2018; Marrano et al. 2018; LaPlante et al. 2021; Trenti et al. 2021; Flutre et al. 2022). The use of GBS improved the size of the set of SNP (Guo et al. 2019; Flutre et al. 2022) and studies using resequencing are able to obtain millions of SNP (Liang et al. 2019; Wang et al. 2021). The combination of several methods is also a good way to increase the SNP coverage (Flutre et al. 2022). Another method using specific locus amplified fragment (SLAF) sequences to detect SNP, identified a set of 414,223 SNP (Zhang et al. 2017). Migicovsky et al., (2017) used 6114 NPs from the *Vitis9K*SNP array on 580 *Vitis* accessions from the USDA germplasm collections in Davis, CA, and Geneva, NY and for 33 traits. But the low marker density and the population structure hindered marker detection for most of the traits. They then used traits selected during domestication like flower sex to focus on genetic area with extended LD due to selection. They were able to find QTL for these traits showing the importance of considering LD as major indicator in genetic studies. Most of traits investigated in GWAS on grapevine are berry related traits or aromas and only two GWAS have been carried out on biotic stress (Trenti et al. 2021; Wang et al. 2021) and one on physiological insight related to water stress (Flutre et al. 2022) (Table 1.1). Most of the time in these studies, genes are explored in the confidence interval that surround the marker detected but functional validations are not carried out. It transcends the higher interest of GWAS in breeding rather than understanding the physiological mechanisms that arise from the genetic region associated with the trait variability. No GWAS has been carried out for root traits or on wild species American genetic background. Despite the interest of rootstocks in grapevine

adaptation (Ollat et al. 2016) and the evidence of a large genetic diversity existing in American *Vitis* genetic backgrounds (Péros et al. 2021), rootstocks remains poorly studied at the genetic level and no GWAS can be found on a specific American specie.

1.2 Take root to grow firmly, to become established

Root system fulfills many functions for the plant; it is the anchorage system, it manages mineral and water absorption and is a storage organ as well (Lynch 1995). In the context of climate change, the studies of root systems are often associated with the soil water availability, temperature, and chemical composition (nutrients and salt concentration) (Sánchez-Bermúdez, del Pozo, and Pernas 2022). Root systems vary widely across species and environment at different levels: anatomy, growth, architecture and physiology. Moreover, these traits are closely dependent of environmental stimulation and impact the vegetative growth and development.

1.2.1 Root anatomy and growth

1.2.1.1 *Internal root organization*

The root is a cylindrical organ organized **radially** into two main parts, the cortex and the central cylinder at the first stage. The **cortex** is devised from the external to the internal by the epidermis, the cortical parenchyma and the endodermis. The **central cylinder** is composed by the pericycle that surrounds the conducting vessels (protoxylem and protophloem; Dolan et al., 1993). Then different areas can be found along the root **axially**, the zone of cell division, the zone of cell enlargement, the zone of cell differentiation and the zone of maturation. (Figure 1.3).

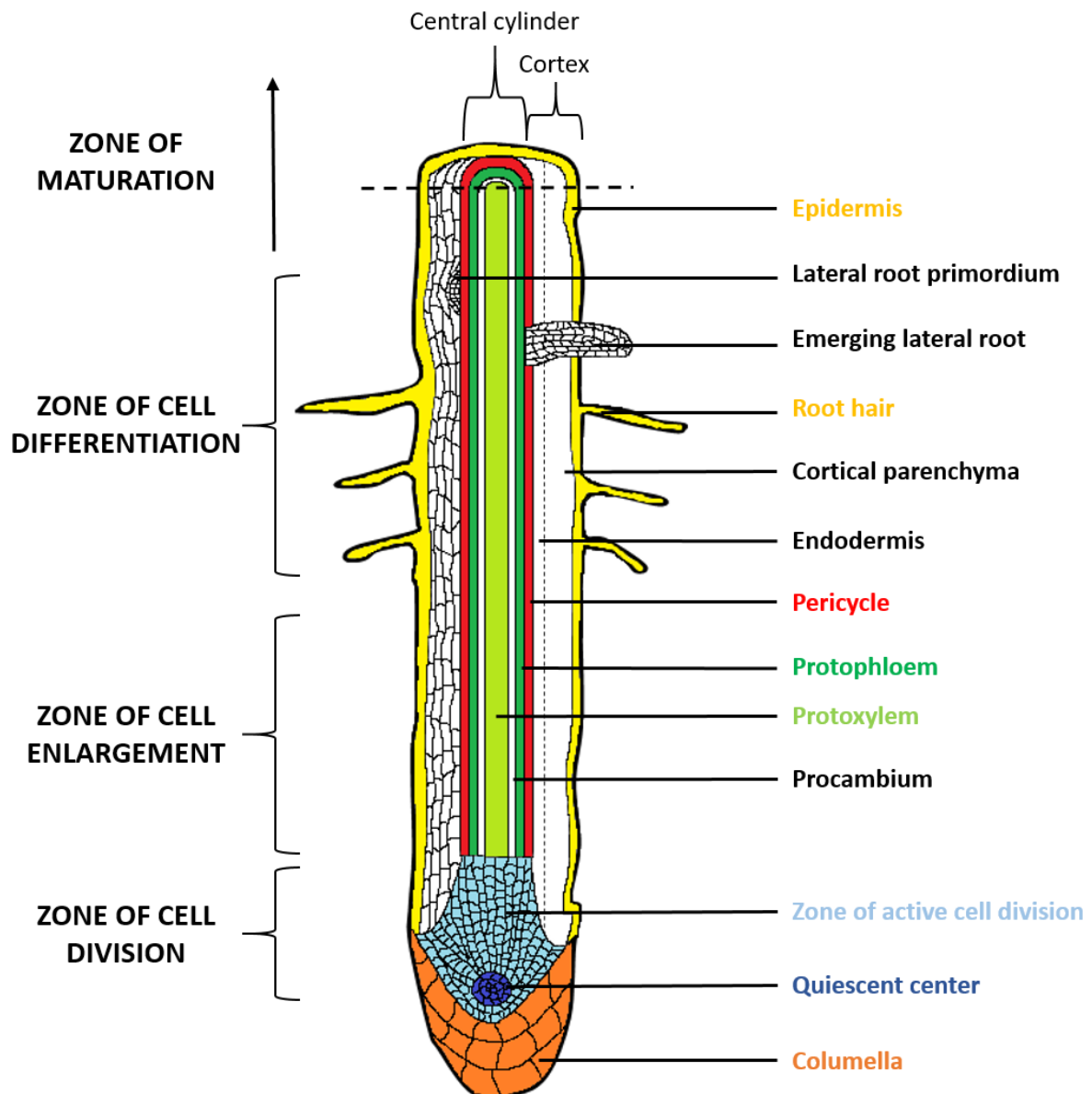


Figure 1.3: Internal root tip anatomy Adapted from Archer et Saayman (2018).

At the seedling stage, the root system originates from the basal domain with the differentiation of the **quiescent center (QC)** and the **columella** root cap (Dolan et al. 1994; Scheres et al. 1994) as it has been shown with *hbt* and *monopteros* *Arabidopsis* **mutants**. In strong *hbt* *Arabidopsis* mutants, the aberrant development of the basal domain leads to the absence of recognizable QC and columella cap cells (Willemsen et al. 1998). In *monopteros* *Arabidopsis* mutants, the basal domain differentiation deficiency leads to the absence of morphological axis and defective root and hypocotyl formation due to aberrant cell division

pattern (Berleth and Jurgens 1993). These mutants make it possible to identify the origin of the root system at the first developmental stage of the seed.

The QC contains four cells in *A. thaliana* surrounded by initial cells which divide into one initial cell and one daughter cell (asymmetric division). Daughter cells have a low division capacity and will differentiate further according to their **location** (van den Berg et al. 1997; van den Berg, Weisbeek, and Scheres 1998). It has been shown that an ablation of the QC leads to a **mitotic arrest** of the columella initial cells in contact with the ablated QC cells and a **replacement** of QC by cells from the **stele** (van den Berg et al. 1997). It has also been observed that QC inhibits the differentiation of the contacting cortical and columella initial cells. Genes involved in root cells division and differentiation have been explored thanks to various *Arabidopsis* mutants allowing to better understand the formation of **apical-basal, radial and circumferential patterns** (van den Berg, Weisbeek, and Scheres 1998). The initial cells are organized into three levels as it has been observed in Solanaceae, Brassicaceae, Asteraceae and others. The columella comes from the lowest layer of initial cells, the epidermis is derived from a collar of initial cells around the columella initials and the higher layer of initials cells gives the cortex and endodermis. The cortex and endodermis come from the same initials and, thanks to the contact with mature cells, the daughter cell asymmetrically divides into cortex and inner endodermis (van den Berg et al. 1995).

Then, during the **secondary thickening** the three outer layers are lost and new cells arise from the stele of primary roots (Dolan et al. 1993). Parenchymal cells create a vascular **cambium** with an oval ring form with phloem on the extremities and xylem inside. Phloem transports carbohydrates in the root for growth and storage as well as hormones implied in root growth regulation. The xylem is composed by different elements, **xylem vats** which are dead cells allowing the transport of water and nutrients by capillarity and root pressure, then by suction when the leaf transpiration become strong enough. **Xylem fibers** are hardly lignified and strengthen the tissue. **Living xylem cells** are involved in storage of carbohydrates and waste products of metabolism (Dolan et al. 1994).

The formation of **secondary roots** comes from a reset of **pericycle** cells which restart mitosis after **auxins** accumulation, creating a new root with a similar pattern as the primary root (Dolan et al. 1993). The amount of lateral roots increases with the addition of auxin (Celenza,

Grisafi, and Fink 1995). **Roots hairs** come from epidermic cells differentiation. Two type of epidermic cells coexist, one is **hairless** and large (**atrachoblast**) and the other, called **trichoblast**, is smaller, richly protoplasmic and form the hair at maturity (Cormack 1949). Different *Arabidopsis* mutants are available for epidermic cells differentiation like *ttg* and *gl2* resulting in hairy epidermic root cells only.

The organization of root systems tissues differs according to the species observed, leading to different **structures** and **anatomies** (Figure 1.4). Various root types are observed in different monocot plants like maize and rice (Hochholdinger et al. 2004). In maize and rice, the root system exchange is enhanced thanks to the **rhizoheath** which corresponds to narrow spaces in the soil linking root hairs and **rhizobacteria**. This system is rarely observed in dicot like *Arabidopsis* which presents only one type of emerging roots which are primary roots and secondary roots rise later in the development. The existence of differences in root anatomy, growth and development across species, genotypes and even in the same root system (Lynch 1995) makes it difficult to transpose information acquired on *Arabidopsis*, which presents a very simple root system, to crops and perennial plants.

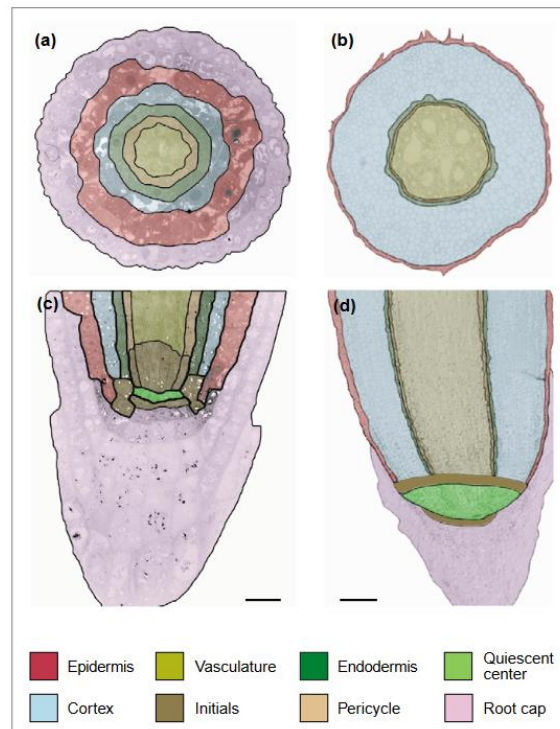


Figure 1.4 : Anatomical organization of the *Arabidopsis* (a,c) and maize (b,d) primary root in median longitudinal (c,d) and transverse (a,b) sections, showing the different cell types and their relative positions. Notice that the upper margins of (c) and (d) represent the longitudinal positions of the root from where the transverse sections were obtained. The images are light microscopic (b, d) and electron microscopic (a, c) photographs that have been colored. Electron microscopic photographs of *Arabidopsis* were provided by York-Dieter Stierhof (University of Tübingen). Adapted from (Hochholdinger et al. 2004).

1.2.1.2 Root growth mechanism and regulation

Root growth depend of cell **division** involved in several process. New cells are generated in each meristem thanks to **asymmetric** initial cells divisions. Meristems are maintained to ensure cell production. Then the organization of cells in roots leads to variations in **morphogenesis** leading to variations in shapes, thickness, length orientation etc. The **root system architecture** corresponds to the **geometric** description of the shape of the root system. Because the soil resources are not evenly distributed, the root system architecture can impact strongly the resources potentially available for a plant which impact in turn its potential productivity (Lynch 1995). Root angle, diameter and length are the most studied traits to characterize root **anatomy** (Wasaya et al. 2018).

Root angle varies according to the amyloplast accumulation (**statolith**) which sediment with gravity in the columella of primary root tips. The accumulation of amyloplast leads to accumulation of **auxin** and then limits the growth of the lower side of the root orienting the growth downward (Ge and Chen 2019). Secondary roots are less sensible to gravity, allowing a radial expand of the root system in the soil. It has been proposed that **cytokinins** are “anti-gravitropic” determinants in roots (Waidmann et al. 2019) and the unequal distribution of this hormone in primary and secondary roots can explain the variability of the gravity responses of the root system.

Root **diameter** represents a strong interest because the objectives of thick and fine roots are not the same. Thick and woody roots constitute a long-term investment in charge of transport, nutrient storage and spreading the root system in the soils layers (Comas, Bauerle, and Eissenstat 2010). Fine roots are involved in nutrient and water absorption in favorable soil areas, represent a short-term investment (Gordon and Jackson 2000), and can be replaced according to environmental conditions.

Root **length** is of major importance in root system architecture, it traduces the potential distance travelled by the root system from the trunk. Then, root length impacts the water and nutrients potentially reachable by the plant. Then root length and root angle correspond to the potential root depth.

Root system growth and development are linked to **hormonal equilibrium** and closely related to vegetative growth (Bouard and Pouget 1971; Taiz and Zeiger 2002).

Auxin is mainly produced in the vegetative part of the plant and then transported in the phloem sap to the roots. At a low concentration, it promotes root and shoot growth. When the **auxin's** concentration increases, it leads to ethylene synthesis which inhibits root growth.

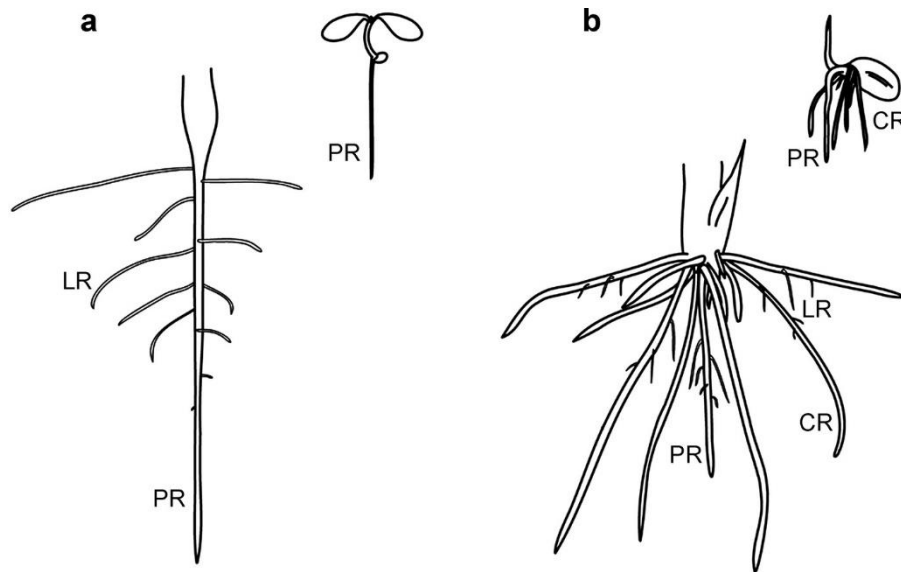
Root system is a principal location of **cytokinins** biosynthesis. Cytokinin is involved in cell division leading to plant growth and inhibition of secondary root formation (Osmont, Sibout, and Hardtke 2007). This hormone is involved in the induction of flower and chloroplast formation. Cytokinins is also involved together with **auxin** in apical dominance and lateral shoot growth.

Gibberellic acid (GA) is synthesized mainly in roots (Scott Russell 1977) in an inactive form and are activated after transport with a wide range of functions. Cell elongation is influenced by gibberellins produced directly close to their site of action in the elongation zone and stimulated by auxin.

Abscisic acid (ABA) is synthesized in root tips as well as in leaves (Taiz and Zeiger 2002) and has an impact on secondary root growth; however, a high concentration of ABA maintains the secondary roots in a dormancy state (Malamy 2005). ABA promotes root growth and inhibits shoot growth allowing to the plant to limit the leaf area in order to reduce the transpiration rate and promote root growth in order to reach deep soil layers to access water resources. ABA biosynthesis is increased by water stress, salinity and nutrients shortage (Scott Russell 1977). It also regulates stomatal closure during water stress events.

Ethylene is present in all parts of the plant, it inhibits root elongation, stimulates the development of lateral root and root hairs and is involved in fruit ripening (Vandenbussche and van der Straeten 2012).

Root growth is governed by the balance between cells **proliferation** and **differentiation** which depends largely on the species considered. Then, different type of root system architecture can be observed like the **allorhizic** root system architecture in **dicotyledons** and **homorhizic** root system architecture in **monocotyledons** (Figure 1.5).



AR Osmont KS, et al. 2007.
Annu. Rev. Plant Biol. 58:93–113

Figure 1.5 : Schematic representation from (Osmont, Sibout, and Hardtke 2007) of (a) typical dicotyledon allorhizic root system architecture (5 and 12 days old *Arabidopsis*) compared to (b) typical monocotyledon homorhizic root system architecture (7 and 14 days old rice). The root types indicated are primary root (PR), lateral root (LR) and crown root (CR).

A. thaliana root system has been widely studied. The first mutants studied for root growth reduction were **shortroot** (*shr*) and **scarecrow** (*scr*) resulting in embryonic and postembryonic **asymmetric** divisions. Both mutations led to a reduction in root growth by affecting different tissues. In the *scr* mutant, one cell layer is missing because of abnormal asymmetric division of cells involved in the **cortex** and **endodermis** formation leading to disturbance in the **radial** organization of the root (Scheres et al. 1995; Di Laurenzio et al. 1996). In the *shr* mutant, the **endodermis** layer is missing and less cells have been observed in the **stele** (Benfey et al. 1993). It is important to note that other *Arabidopsis* mutants have shown deficiencies in root growth with tissue specific origin or not (Benfey et al. 1993), showing the importance of genetics in the root development. According to information found on the TAIR platform (Huala et al. 2001), orthologs genes have been found for *shr* and *scr* in cultivated species such as maize, rice, banana, sorghum, populus, prunus, tomatoes and others. It shows that functional information found in model species can be applied to others species. However, according to the degree of relationship between species, orthology is not necessarily linked to the conservation of gene function (Gabaldón and Koonin 2013).

Root **diameter** is highly variable across species with **apex** diameter from less than 100 μm (poaceae, juncaceae, cyperaceae) to 1 mm (magnolaceae). The **thickness** of roots has different physiological impact like modifications in root **hydraulic conductivity**, thinner roots having a higher hydraulic conductivity and then a higher **transport capacity**. Rieger et Litvin (1999) have calculated the root hydraulic conductivity of 5 species (asparagus, dendrobium, soybean, peach, sour orange) showing that hydraulic conductivity is negatively correlated with root and **cortex** diameters with variations up to 8 fold across the 5 species. The root thickness is also linked to the **mychorrization** ability, **perennials** and **thick rooted** plant being more **mychorrized** than fine roots (based on 968 species of the British flora; Peat et Fitter 1993).

In **perennials** (*P. halepensis*, *P. pinea* and *T. articulate*), differences in root **stele** diameter have been observed according to species and root depth (Oliveras et al. 2003). These results have been confirmed later on by Wang et al. (2016) on *J. mandshurica*, *F. mandshurica* and *P. amurense* (Figure 1.6). They have also observed significant differences in root diameter according to the species. Even in the same plant, **root growth** rate varies widely. It has been observed on Oak seedling that lateral roots grow rapidly first and then stop growing. Roots with lower growth rate continue to grow for a longer time and reach a higher final length (Pages 1995). The main difference seems to be the root apex diameter, small apex diameter leading to reduced root growth (Pages 1995).

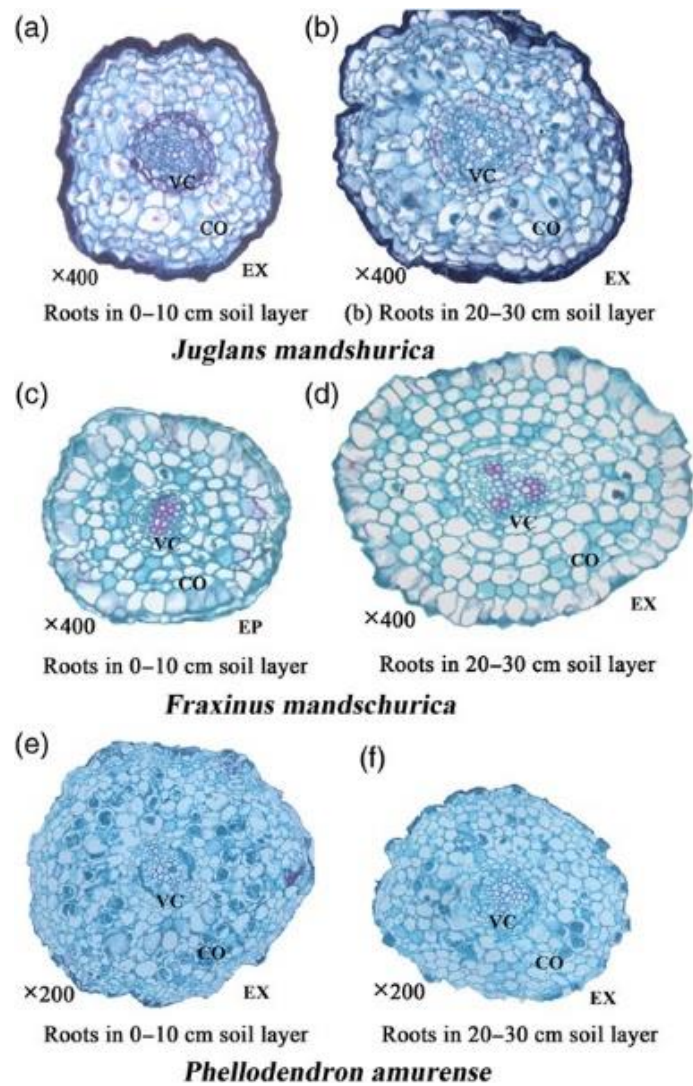


Figure 1.6 : Typical anatomical structure of the first-order roots at surface (0–10 cm) and subsurface (20–30 cm) soil layers in tree species: *J. mandshurica*, *F. mandshurica* and *P. amurense* plantations. EP, epidermis; EX, exodermis; CO, cortex; VC, vascular cylinder (stele). From Yan Wang et al. (2016).

While, root systems are largely affected by environment, the variability due to genetics is important to consider and more precisely the interactions between genetic and environment.

1.2.2 Environmental relationships

1.2.2.1 Impact of soil conditions on root morphology and physiology

It has been shown that root growth is closely related to the **soil texture**, **chemical composition** and the **water** available in soil layers. The **concentration** in **minerals** has an impact on root growth and fine root death. The absorption of nutrients and water is made mainly by passive process with osmotic gradient between soil and roots. Because cell walls are negatively charged, cations can be absorbed faster than anions. Moreover, active transport also occurs to absorb nutrients against the osmotic gradient. The soil **structure** and texture have a strong impact on root growth and development. Roots have a better growth in rich, porous, deep, and wet soil layers. The morphology of the root system is largely dependent of chemical and physical soil characteristics, structure being more important than texture (Seguin 1972).

Water moves into the root from epidermis to endodermis through several mechanisms (Taiz et Zeiger 2002; Figure 1.7). The **apoplastic** pathway corresponds to water flow in cell walls, blocked by the Casparian barrier in the endodermis. To move into the xylem, water can only pass through the protoplasm of endodermis cells. The trans-membrane pathway, in which water cross cell walls going into the cells from one side and go to the next cell by the other side. The last water transport is the **symplastic** pathway which is protoplasmic, water progresses radially into the root in a cell to cell way using plasmodesmata. **Aquaporins** have been identified as key factors to favorize water flow in roots (Maurel et al. 2015). Then water reach leaves through xylem. Whenever the transpiration of leaves is sufficient, tension is applied from the vegetative part to the soil, increasing the absorption power of the root system and the tension in xylem vessels.

The heterogeneity of water resource in soil shapes **the root system architecture** in different ways. (Bao et al. 2014; Orosa-Puente et al. 2018) have observed **hydro-patterning** or the root system in *Arabidopsis*, maize and rice. The root branching occurred from the watered side of the main root through auxin signaling. This phenomenon is coupled with the **xerobanching** of the root system, mediated by ABA accumulation in root areas which are not in contact with water leading to branching inhibition (Orman-Ligeza et al. 2018). Moreover, the **hydrotropism** also has an impact on the root system growth, leading to the orientation of root towards wet

soil zones and dependent of auxin signals in the cortex of the elongation zone (Dietrich et al. 2017).

Salt concentration in soil impacts root architecture by the **halotropism** response which corresponds to the orientation of the root system to avoid high salt concentration areas in the soil by relocalizing auxin in the root tip thanks to PIN2 transporter (Galvan-Ampudia et al. 2013). This negative **halotropism** has been observed in Arabidopsis, tomato and sorghum which are salt sensitive (Galvan-Ampudia et al. 2013). Positive halotropism has been observed on root systems from other species like *Bassia indica* (Shelef et al. 2010) or *Limonium bicolor* (Leng et al. 2019). Moreover, 2 genes (CHX13 and DOB1) associated with the halotropic response in Arabidopsis were detected (Deolu-Ajayi et al. 2019).

1.2.2.2 Impacts of water scarcity on root systems

Whenever warm and dry period are accompanied with low water availability, the tension in xylem vessels can create bubbles or **embolism** (Tyree and Sperry 1989). Small roots are more susceptible to cavitation than thick ones (Sperry and Ikeda 1997).

A few root traits have been proposed as good targets for **drought tolerance** like reduced root diameter, higher specific root length, and higher number and/or length of root hairs which could improve water acquisition with a low carbon investment (Comas et al. 2013). Because soil start drying from the shallower soil layers, root depth is also a trait of major importance for drought tolerance (Lynch 2013). It has also been suggested that resistance to cavitation could increase water deficit tolerance in maize (Cochard 2002) and in perennials woody plants (Delzon and Cochard 2014).

In grapevine, the drought stress led to mechanical failure, fine roots reducing their hydraulic conductance (Cuneo et al. 2016). First, cortical lacunae were observed, then embolisms were formed leading, if the drought stress was ongoing, to root death. Fine roots are more responsible for water and nutrient absorption even though large roots are able to absorb water whenever fine roots are scarce (Cuneo et al. 2018). The fine root are the first damaged roots during drought events but older ones are damaged when the stress increased. The impact of root death can be compared to root pruning in Smart et al., (2006a) who have observed a decreased stem and pre-dawn water potential in pruned plants. Their leaf gas

exchange was 40% lower than unpruned plants and leaf expansion and final area were reduced. The root survivorship can also be a trait of interest for root system architecture variability. Bauerle, Richards, et al. (2008) have observed the water redistribution in the root system from wet zone to dry ones during period of low evaporative demand. This mechanism allowed observing a higher root survivorship and limited electrolyte leakage (Gambetta et al. 2013; Charrier et al. 2016; 2018).

Finally, several phenomena have to be considered in the case of water deficit (Figure 1.7). Root system architecture allows to access water resource in the soil. When water is scarce, the **tension** in xylem vessels increases until the closure of leaves **stomata**. It is then easy to understand that a lot of traits can improve water deficit tolerance in plants like the root **depth**, **diameter**, sensibility to **cavitation**, impact of inner **anatomy** on the water absorption efficiency, fine root **survivorship** and **redistribution** or the **hydraulic conductance** of the root system etc.

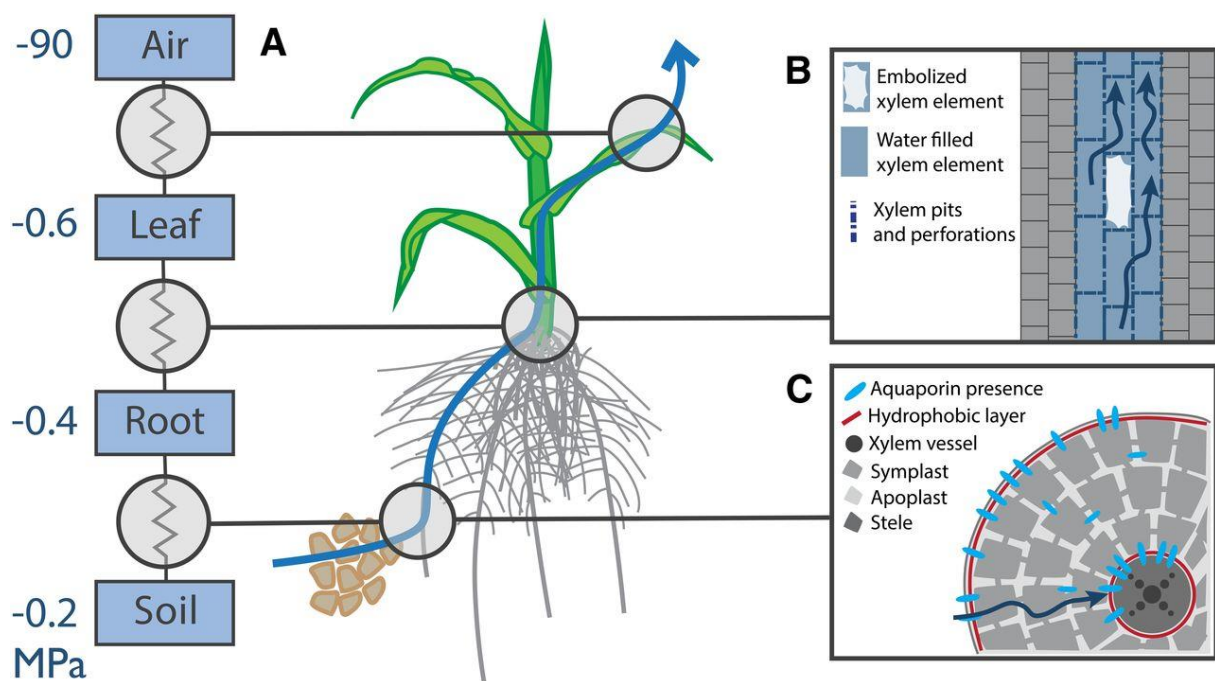


Figure 1.7 : Water flow in the plant from (Lobet et al. 2014).

1.2.2.3 The salt stress on root systems

Salt stress produces water stress and nutrient imbalance because of the low water potential of saline soils. It leads to a reduced root mass, limited root elongation and modifications in root architecture (van Zelm, Zhang, and Testerink 2020). In response to salt stress, suberin accumulation is a barrier in root endodermis to limit salt impact on roots (Wang et al. 2020) as well as lignin accumulated around mature xylem tissues (Liu, Luo, and Zheng 2018).

In grapevine, salt stress induces a decrease in **yield** and alteration of **berry development** and **composition** on own rooted plants (Prior, Grieve, and Cullis 1992; Walker et al. 2002; 2004). Salt tolerance varies widely between grape rootstocks. Some rootstocks reduce the impact of salty soils on grapevine yield and berry quality providing a good way of adaptation for vine growers (Ollat et al. 2016; Walker et al. 2004; 2002; Zhou-Tsang et al. 2021).

Finally, root system architecture is the result of the **interaction** between plant **genotype** and **environment**. Environmental conditions impact plants root growth, shaping the root system with root depth (**hydrotropism, halotropism**) or root density (**xerobanching**). The genetic part of the root system architecture variability can be observed by measuring root traits on several genotypes in a similar environment as in common gardens.

1.2.3 A huge diversity in root systems profiles

1.2.3.1 Genetic variability of root traits

At the phenotypic level, variability has been observed for root-related traits in Arabidopsis (Pacheco-Villalobos and Hardtke 2012), annual crops (Deja-Muyllé et al. 2020; Maqbool et al. 2022) and perennials (Nielsen 1992; Wullschlegel et al. 2005; Krabel et al. 2015). The **genetic determinism** of few root traits has been identified previously, all **morphological** traits like root length, root diameter, root density or root angle can be associated with root system architecture. For example, the DRO1 (deep rooting) QTL has been identified in rice RILs (Uga, Okuno, and Yano 2011) on chromosome 9 explaining 67% of the variability of the ratio of deep rooting (proportion of roots going deep through the basket bottom). DRO1 is negatively regulated by auxin and an increase in DRO1 expression leads to higher root angle. Modifying root angle led to avoidance of drought stress and then maintained high yield performances

despite drought conditions (Uga et al. 2013). A homolog of DRO1, qSOR1 control the root growth angle and has been used in rice to obtain introgression lines with varied root growth angles leading to four different root phenotypes (*ultra-shallow, shallow, intermediate, and deep rooting*, Kitomi et al., 2020). In this case, the qSOR1 is a loss of allele function leading to rice with surface roots allowing to limit the saline stress in the soil and leading to an increase in yield. In cotton, Cui et al. (2022) carried out a GWAS on 38 root-related traits. They have obtained **high heritability** for all traits (>90%) and a coefficient of variation from 7% up to 200%. Two major regions were associated with root length, surface area and root diameter and two candidate genes were validated by silencing (*GhTRL1* and *GhPIN8*). In rice, Courtois et al. (2009) used the quantitative genetic results from 24 studies related to 29 root traits. Because the same population was used in different studies, 675 QTL from 12 mapping population were used (doubled haploid population and recombinant inbred lines). This **meta-QTL study** revealed QTL co-localizing for root trait under stress and favorable conditions increasing the reliability of these QTL (see 1.1.2.). Moreover, this study reduced the QTL confidence interval detected in several studies. In maize, another meta-QTL study carried out (Guo et al. 2018) for 23 root-related traits and in 20 studies revealed 53 meta-QTL involved in root system architecture. In these regions, 3 genes were identified as being associated with lateral and crown root development and 2 genes were associated with nitrogen and phosphorus stress responses. Later on, Guo et al. (2020) carried out a GWAS on 209 maize accessions for seminal root length under water stress and well-watered conditions. In this study, 62 SNP were identified (27 under water stress condition and 35 under well-watered condition) for seminal root length. **Transcriptomic analysis** allowed them to combine information from GWAS and from differentially expressed genes for the two treatments to highlight 7 genes putatively involved in seminal root growth under stress conditions.

In woody **perennials**, root system architecture and anatomy have been explored, revealing a large **diversity** in root system profiles with a **high potential heritability**. Krabel et al. (2015) have observed a high variability in the length of the longest root and the dry biomass of the root system across seven poplar hybrids. Nielsen (1992), observed **contrasted** root profiles for two Picea trees species. The variability was observed at the **inter** and **intra clonal** levels. Differential root/shoot ratio were also observed with a high genetic control (H^2 from 0.73 to 1 according to the calculation method used). In a poplar population (434 progeny) cultivated

in containers phenotyped for 12 adventitious roots and related shoot traits identified 150 QTL associated with adventitious root traits explaining from 3.1 to 6.1% of the phenotypic variation (Sun et al., 2019). Wullschleger et al. (2005) used two poplar field grown populations and measured stem, branches leaves, cutting, coarse roots and fine roots biomass. They observed variability for these traits in the two families allowing them to detect QTL for all these traits. Variability have been observed for root anatomy traits as well in **angiosperm** at different groups levels (Amborellales, Nymphaeales, Austrobaileyales, Magnoliids, Monocots, and Eudicots)(Seago and Fernando 2013). Finally, while root system phenotype is hard to measure, the variability existing in **crops** and **perennials** compiled with a high heritability are promising to carry out genetic studies on root traits.

1.2.3.2 Are ideotypes definition a dream?

Root system architecture depends on many environmental factors, mainly soil physical and chemical properties, interacting with genotypes. In order to determine which root traits are the most advantageous, root system **ideotypes** have been explored. A root system ideotype corresponds to an optimized root architecture in a specific environment. Lynch (2013) proposed a root system ideotype for N and water acquisition in maize called SCD (steep, cheap, and deep). It corresponds to a low carbon cost root system with diving deep roots in order to optimize the soil layers exploration by the root system to access deep resources with low investment of carbon resource. This root system ideotype is proposed for maize and more extensively to cereals and dicots. It is important to note that an ideotype for perennial plants should be different because their root systems represent a carbon reserve for new vegetative organs development each year. Moreover, in perennials the carbon resources invested one year in main roots will be beneficial for the plant the next years.

The cost of the root growth compared to benefit for the plant is one of the main criteria for evaluating root system adaptation. According to the soil characteristics, the same performance can be cost-effective or not. Two models based on resources availability are discussed by Lynch (2018), *high* and *low* input agroecosystems which lead to different needs in term of root architecture. In *high* input agroecosystems, the root system doesn't need to develop a lot but has to be efficient in water absorption. On the other hand, in *low* input

agroecosystems, the root system has to develop more in order to reach deep soil layers and explore larger soil areas. The contrast between mobile (N, water) and non-mobile (P) resources is also discussed in low input agroecosystems because the plant roots have to be very close to non-mobile elements in order to absorb them. This has a strong impact on root system cost-effectiveness which can be then divided into two major components: the cost of **creation** and the cost of **maintenance** which are related to each other (Amthor 1984). The creation cost has two carbon components, the carbon used in the dry mass and the carbon used in the respiration directly correlated to the growth rate (Lambers 1983).

The **transport** cost has also to be considered, that cost is associated with the resistance due to the hydric potential which increases with distance (Hacke and Sperry 2001). The emergence of a new root or the growth of roots increases the distance between root tip and leaf and thus increases transport cost. However, it also allows roots to explore a new soil area which can be cost-effective. In term of transport cost, secondary roots are most cost-effective because they increase the soil volume explored without increasing the distance of transport.

To resume this section, root system **ideotypes** are hard to define and largely depend on the plants species and soil properties. Because of the unequal repartition of soil resources, the root system architecture plasticity can be advantageous in low input agroecosystems (Lynch 2018). However, the **plasticity** of root traits induces a large potential variability in root system profiles, which makes it complicated to identify the most important root traits to target in breeding programs. One of the current goals in root system studies is to highlight which traits have to be targeted in breeding and what are the impacts of these traits on the entire plant phenotype. Once the root traits targets have been identified, breeding programs have achieved water deficit tolerance as in common bean (Burridge et al. 2019).

1.2.4 Grapevine (*Vitis spp.*) root systems variability depends of the rootstock

The grapevine root system starts growing by emitting the first root (radicle) which forms the primary root after seed imbibition from which secondary roots will form. This is a classic root morphology in dicotyledons called **allorhizic** root system (Figure 1.5A). Because grapevine is cultivated with a vegetative propagation, the root system starts from the last node of cuttings leading to a root system architecture more similar to **homorhizic** morphology (Figure 1.5B, (Pratt 1974). Each root starting from the nod is considered as a primary root that can branch producing a complex root system composed by secondary, tertiary, etc. roots. Moreover, grapevine is able to produce new lateral roots from old part of the root system in contrast with other species, which allows to increase the soil volume explored by the root system (Keller 2015) and lead to more complex root system architecture.

As for other species, it has been observed that the **distribution** of roots in the soil depends of soil properties but the **density** is mainly linked with rootstock (Mullins, Bouquet, and Williams 1992). The **depth distribution** of vine roots is more affected by soil properties than by genotype (Smart, Breazeale, and Zufferey 2006), but they suggested to analyze the **root angle**, which could be more genotype dependent and lead to plunging root system explaining scion vigor and drought tolerance. Smart et al. (2006b) compared rooting patterns observed with trench-wall profiles of 40 different *Vitis* and *Muscadinia*. The soil texture had a small effect on **root depth**, but soil structure, stoniness and the depth of the water table had a strong impact on root vertical **distribution**. They observed variability for root biomass or root distribution at different depths between *Vitis* species.

Thus, soil properties are very important because of their impact on the grape root system development which in turn impact the vegetative growth and plant yield. Soil texture and structure are not the only factors that affect the root system distribution. The temperature of the soil impacts the architecture of the root system as it has been shown with the Shiraz variety (Clarke et al. 2015). The increased soil temperature led to higher root density and branching, and then to a faster life span, larger leaves and higher shoots. The clay content has also been identified as shaping the grape root system (Battista et al. 2016). They studied the

impact of soil clay content on grapevine root distribution in soil layers. The high clay content led to a more superficial root system and non-homogeneous root distribution across soil layers. Moreover, the unequal distribution of roots in soils have been correlated with yield fluctuations across years.

Moreover, the root system architecture of grapevine varies across the **season**. Zyl (1984) observed that the root growth cycle of grapevine is divided into **two growth periods** per season at flowering and harvesting time (Figure 1.8). This **bimodal** pattern of root growth avoids competition with shoot and clusters growth for carbon resources. However, variability in this pattern has been observed with different rootstocks and different years while most of the root appeared between flowering and veraison (Eissenstat et al. 2006). The root system development and growth depends also of root death which occurs when fine roots are in an unfavorable environment as it has been observed for water scarcity (Cuneo et al. 2016).

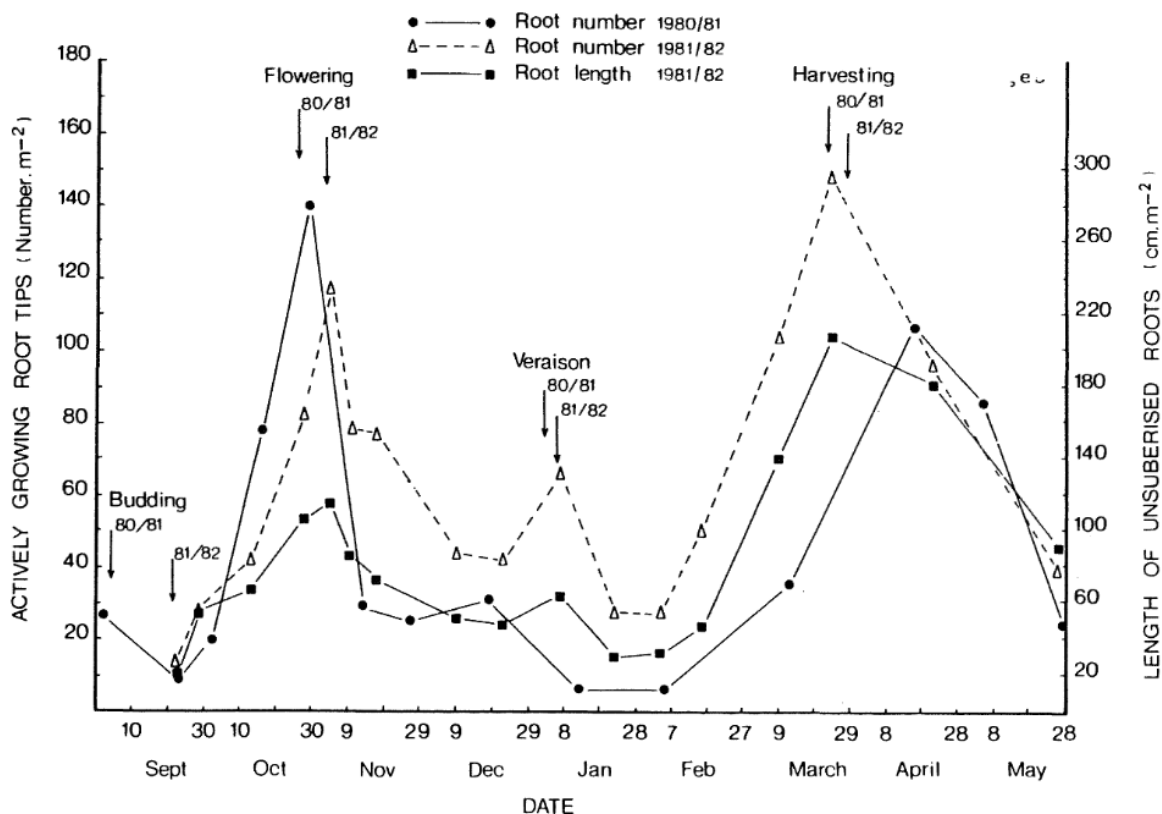


Figure 1.8 : Colombarid root length and formation during a season from (Zyl 1984)

Since the phylloxera crisis, grapevine is cultivated grafted. Rootstocks use to be hybrids between American species (mainly *V. rupestris*, *V. riparia* and *V. berlandieri*) and sometimes *V. vinifera*. The use of rootstocks first allowed the plant to acquire tolerance to phylloxera.

Then it has been shown that rootstock and scion interactions promoted use of the rootstock genotype to make adjustments on the scion part, the main criteria being water stress tolerance, conferred vigor, limestone tolerance and phylloxera tolerance (Galet 1988). Thus, root systems of cultivated grapevine can have a wide range of genetic origin and the interactions between rootstocks and scions promotes rootstocks use as a good way for grapevine adaptation (Ollat et al. 2016).

A huge **genetic diversity** exists in rootstocks (Péros et al. 2021) which can be observed at the phenotypic level. Thus, the responses of rootstocks to environment variability is not the same and the response of the root system varies between varieties. Under limiting water conditions, several rootstocks (110 R, 140 Ru, 1103 P, 41 B and SO4) have shown diverse responses for root and vegetative traits (Peiró et al. 2020). 110 R was the more tolerant rootstock because of its ability to sustain vegetative growth in response to water stress. Yildirim et al. (2018) observed differences in root system development in 3 rootstocks (110R, 5BB and 41B) grafted with Sultana seedless (*V. vinifera*) in response to water limitation. The root area, root length, ramification and number of root tips were more reduced for 5BB and 41B than 110R. Root relative water content and total carbohydrate and nitrogen content was higher in 110R roots. Transcriptomic analysis revealed regulatory pathways involved in root elongation and enlargement impacted by drought. These three transcriptomic pathways are involved in sugar and protein transport (SWEET and NTR1/PTR), osmotic adjustment (ehydrins, Glycine-proline rich proteins, LA proteins, osmotins...) and root suberization (Caffeic acid 3-O-methyltransferase, eceriferum 3 and 3-ketoacyl-CoAsynthase) showing the potential improvement of grapevine for drought adaptation at the rootstock genetic level. Alsina et al. (2011) have compared drought responses of two rootstocks grafted with Merlot. One rootstock was considered as sensitive to drought (101-14 MGt) and one as drought tolerant (1103P). The drought tolerant rootstock grew roots to a greater depth during the dry period, allowing the scion to maintain a higher transpiration rate. Moreover, the root system conductance was higher for the tolerant rootstock without significant changes in root anatomy. Then, there was neither transpiration regulation from the rootstock nor anatomy modification. It is proposed that root architecture, and mainly root depth led to a higher tolerance of the entire plant against water stress. In this study, the variability of rootstocks performances under drought conditions can be explain by a better root growth in depth during

non-limiting water conditions, leading to the access to deeper water resources. Thanks to the transpiration maintenance, root growth can continue during water limitation period allowing to go on with soil exploration. Other strategies can be observed in term of rootstock tolerance to drought, as limiting water loss during dry period by limiting transpiration or by root osmotic adjustment (Serra et al. 2014). Various other traits have shown variability between rootstocks like root survivorship (Bauerle, Smart, et al. 2008), root density (Smart et al. 2006), nutrients absorption (Kidman et al. 2014) bud fertility or carbohydrates storage (Cox et al. 2012). The variability observed for these traits can be related with plant adaptation to external factors and traduces the plant root system plasticity.

The grapevine root system architecture remains poorly studied but a few traits have been highlighted as being favorable for the plant in the majority of environment. These traits are linked to the soil area explored by the root system (Lynch 1995). Increasing the root density in deep soil layers seems to be of major interest to access deeper resources and then maintain a favorable plant water status (Lynch 2018). It is important to consider the root system architecture of the plant before facing stress (constitutive) as well as how do they react to it (adaptation).

As well as the rootstock impact the **scion growth**, development and its responses to environmental variations, the scion has an impact on rootstock traits. Comas et al. (2000) have observed variability in root death rate on grafted grapevines after shoot pruning. Later on, Comas et al. (2005) have also highlighted links between canopy management and the timing of root production. These results were confirmed by Tomasi et al. (2020) who observed an increased root growth and density for 13 years old vines pruned during winter. The sugar content was higher for pruned vines as well. They suggested that the ratio shoot/root resources allocation is unbalanced because of pruning, leading to more carbohydrates allocated to the root allowing a better growth and development of the root system. The carbohydrates storage in the root system of woody perennials is of major importance for their growth, development and survival over seasons (Loescher, Mccamant, and Keller 1990).

1.2.5 Root and shoot achieving balance

1.2.5.1 Root and vigor

Because root system profiles impact plant water and nutrient uptake, the **vegetative growth** of the plant is also impacted by the root system. Montpetit and Coulman (1991) have identified significant correlation between the amount of adventitious roots and the spring **vigor** in red clover for five different root profiles. In wheat, Yinglong et al. (2020) have observed moderate to high variability in 24 root traits as well as 4 shoot traits. Several root traits, including root dry weight at different depths were significantly correlated with shoot traits such as the shoot dry biomass or the tiller number at early vegetative stage. Still in wheat, the root number of plants have shown a **high broad sense heritability** and was associated with vegetative dry mass under compacted soils (Colombi and Walter 2017).

It is then possible to select genotypes with favorable root system for specific constraints like water stress in order to improve or maintain yield despite water deficit events. To do so, Wasson et al. (2012) proposed a breeding itinerary for wheat genotype selection with deeper root systems and higher radial hydraulic conductivity in order to access deep water resources.

In grafted plants, the scion and the rootstocks are two different **genotypes**. Grafting have been used for hundreds of years (Mudge et al. 2009) and rootstocks are mainly used to modify the scion phenotype for **vigor, precocity, productivity, and fruit quality** (Webster 1995) as well as abiotic tolerance (Warschefsky et al. 2016). The impact of rootstocks on the scion vigor (assimilated to the vegetative growth) is called **vigor conferred**. Khah et al. (2002) observed the effect of grafting on yield and growth in tomatoes, with more vigorous and productive plants in grafted field and green-house grown plants. Leonardi and Giuffrida (2006) also observed modifications in tomatoes and eggplant **vigor** according to the rootstock used in field conditions. They highlighted the impact of rootstock genotype on plant nutrient content. The impact of **rootstocks** on the seasonal root pressure has been studied in kiwifruit (Clearwater et al. 2007), high vigor rootstocks developing greater root pressure early in the season. The authors also highlighted the impact of rootstocks on the precocity of the plant, which is of major interest in fruit market. Clearwater et al. (2006) observed a reduction by 50% of leaf area on low vigor kiwifruit rootstocks compared with high vigorous rootstocks

genotypes. Costes, Salles, and Garcia (2001) studied the impact of apple tree rootstock on vegetative growth. They have observed a significant difference according to the rootstock used. Moreover, the impact of rootstock on the vegetative growth of the tree during the first years of growing was **cumulative**. The authors explained that the increased growth of the plant due to the rootstock allowed it to start growing in better conditions the next year, thus the impact of the rootstock increased year after year. Later on, the authors confirmed the impact of rootstocks on apple tree vegetative growth as well as the cumulative effect of rootstock over years (Costes and Garcia-Villanueva 2007). Rootstocks have also been used for biotic tolerance as it has been done for phylloxera in grapevine (Galet 1988).

It has also been shown that the scion genotype has to be considered in the **rootstock x scion interaction**. In orange tree, different scions grafted on the same rootstocks genotypes have shown different responses in their vigor (Meneses et al. 2020). In the same study, correlations between root distribution in depth and trees vigor, yield, as well as water status were shown. Moreover, the impact of rootstocks on fruit quality and plant productivity have been highlighted in watermelon (Proietti et al. 2008) or grapevine (Tandonnet et al. 2010; Clingeleffer et al. 2019).

Finally, the impact of root-related traits on the vegetative growth and development has been observed previously and there is interest in selecting **genotypes** for root-related traits in order to increase water and nutrient uptake. In grafted cultivated plants, the rootstock is the root system of the plant and the impact of the rootstock on the vegetative growth and development has been observed. However, the mechanisms that occur between the scion and the rootstock remain unclear. Webster (1995) has reviewed this question and noted the difference between the dwarfing effect of a rootstock as an interstock was much lower than used as a complete root system, highlighting the importance of the root system in scion's regulations. Moreover, the mechanisms of the root:shoot ratio are also discussed, because of the impact of root-related traits on plant nutrition, a smaller root system should reduce water and nutrient absorption as well as hormonal and other molecule content leading to a reduced vegetative growth.

1.2.5.2 Root and carbon isotope discrimination

In atmosphere, two stable **isotopes** of C exist (C^{13} and C^{12}) which have differences in their atomic mass, physical and chemical properties. Because of these variations, the lighter form is favored in chemical processes resulting in differences in the atmosphere carbon isotope ratio and the organism composition. In plants, the carbon assimilation occurs during photosynthesis from CO_2 present in stomatal space. The $\delta^{13}C$ is the ratio between quantity of carbon 13 divided by the quantity of carbon 12 in a sample and the reference value, or:

$$\delta^{13}C = 1000 \left[\frac{(C^{13}/C^{12})_{sample}}{(C^{13}/C^{12})_{reference}} - 1 \right]$$

The carbon discrimination is related with the plant photosynthesis (Farquhar, Ehleringer, and Hubick 1989) and is used as indicator of water use efficiency (Farquhar and Richards 1984). During water deficit events, the stomatal closure increases the C^{13}/C^{12} ratio in the stomatal space as the C^{12} is preferentially absorbed (Brüggemann et al. 2011). It is then possible to analyze $\delta^{13}C$ in organs formed during water deficit events in order to compare the intensity of stress faced by the plant during a specific period.

The carbon discrimination distinguished species carbon assimilation behaviors (Bender 1968). Elazab et al. (2012) observed variation in $\delta^{13}C$ in four wheat RILs, they suggested that $\delta^{13}C$ could be a good **proxy** for root traits associated with growth in **well-watered conditions**. Cernusak et al. (2007) studied 8 plants species (*Dalbergia retusa*, *Ficus insipida*, *Pachira quinata*, *Platymiscium pinnatum*, *Pseudobombax septenatum*, *Swietenia macrophylla*, *Tectona grandis*, and *Saccharum spontaneum*) for their water use efficiency. They used the $\delta^{13}C$ information for which they observed significant variation among species. A correlation between $\delta^{13}C$ and the transpiration efficiency of carbon have been observed within species but not across species, highlighting a potential species-specific relation. Variation in $\delta^{13}C$ have been observed in leaves, stem phloem, and roots in three species (*Halimium halimifolium*, *Rosmarinus officinalis*, and *Acacia longifolia*; (Dubbert, Rascher, and Werner 2012), height potatoes accessions (*Ipomoea batatas*; Gouveia et al. 2019), or sunflower (*Helianthus annuus*), alfalfa (*Medicago sativa*), and perennial ryegrass (*Lolium perenne*)(Klumpp et al. 2005).

At the genetic level, $\delta^{13}\text{C}$ variability has been explored in *Arabidopsis thaliana* (Masle et al. 2005, Juenger et al. 2005; Hausmann et al. 2005), in crops such as maize (Gresset et al. 2014) revealing mainly 5 genetic regions involved in the genetic architecture of the trait. This et al. (2010) have highlighted 11 QTL explaining from 8 to 19% of the $\delta^{13}\text{C}$ variability in a rice doubled haploid and recombinant inbred populations issued from the same cross. In wheat, five QTL were associated with $\delta^{13}\text{C}$ using two statistical methods (Wu, Chang, and Jing 2011). In soybean, 16 QTL were identified for $\delta^{13}\text{C}$ explaining from 2.5 to 29.9% of the variability and one major QTL have been highlighted in tomato (Xu et al. 2008). In maritime pine, 8 QTL were detected for $\delta^{13}\text{C}$ and the narrow sense heritability was 0.17 (Brendel et al. 2002). In *Quercus robur*, ten QTL were highlighted for $\delta^{13}\text{C}$ including one QTL highlighted for three independent years and explaining more than 20% of the variance (Brendel et al. 2008). GWAS were also carried out on this trait in soybean (Dhanapal et al. 2015; Steketee et al. 2019) and wheat (Mora et al. 2015).

In perennials, the heritability of $\delta^{13}\text{C}$ has been estimated at 0.29 in *Pinus pinaster* (Marguerit et al. 2014), 9 QTL were identified in a greenhouse experiment, and 2 in a field experiment with one of them explaining 67% of the phenotypic variance. In *Quercus robur*, 10 QTL were detected for $\delta^{13}\text{C}$ whose one was detected over three years of experiment and explained more than 20% of the variability of the trait (Brendel et al. 2008).

Moreover, because of the link between the root-rhizosphere interactions and photosynthesis (Högberg et al. 2008; Barthel et al. 2011), we can expect that root-related traits could have an impact in $\delta^{13}\text{C}$. In the case of grafted plants, rootstocks could impact the $\delta^{13}\text{C}$ in scion's leaves during water deficit events, also traducing variations in water deficit behaviors induced by the rootstock genotype.

In grapevine, the water use efficiency varies between cultivars and represent a way of adaptation to climate change (Tomás et al. 2014). The variability that exist between *Vitis vinifera* cultivars for $\delta^{13}\text{C}$ and its correlation with water status. Measurements on plants grafted on the same rootstock 110R (Bota et al. 2016), 1103P (Chaves et al. 2007), Fercal (Gaudillere, Van Leeuwen, and Ollat 2002). Recently, Plantevin et al. (2022) have studied a large panel of 48 grapevine varieties grafted on SO4 during 6 consecutive years for their drought condition behaviors. They used berry juice $\delta^{13}\text{C}$ as indicator of water deficit tolerance

using hydroscape slopes to characterize each variety. They have shown that $\delta^{13}\text{C}$ values under well-watered conditions were highly correlated with values obtained from hydroscares and suggested that $\delta^{13}\text{C}$ under well-watered conditions could be a very good indicator of drought stress responses. In addition, variability has also been observed for the same cultivar (Tempranillo) grafted with different rootstocks (Mairata et al. 2022). A grapevine study detected QTL associated with $\delta^{13}\text{C}$ measured in leaves in a rootstock population (*Vitis vinifera* cv. Cabernet Sauvignon x *Vitis riparia* cv. Gloire de Montpellier) grafted with the same scion (Marguerit et al. 2012). They observed variability on scion responses to water stress and to $\delta^{13}\text{C}$. This study confirmed the control of scion behavior when facing water deficit conditions at the genetic level. QTL were also detected in a recent GWAS study carried out on a panel of 279 *V. vinifera* cultivars grafted on the same rootstock (Flutre et al. 2022).

Thus, the $\delta^{13}\text{C}$ is a promising indicator of water deficit responses of grapevine in well-watered and water deficit conditions. The impact of root-related trait of this parameter has been observed. In a grafted context, because they define the root system characteristic and they have a genetic control on scion related traits, rootstocks represent a very good driver for grapevine adaptation. However, less studies have explored the $\delta^{13}\text{C}$ at the genetic level, than the phenotypic and genetic variability. Highlighting genetic regions involved in $\delta^{13}\text{C}$ determinism in rootstocks breeding is clearly of interest.

1.3 Objectives and strategy

The grapevine adaptation can be achieved through rootstock breeding at the phenotypic (root-related traits) and the genetic level (genetic determinism of traits of interest). A large genetic diversity has been observed in American *Vitis* genetic backgrounds (Péros et al. 2021). However, these genetic backgrounds have always been studied from germplasm collection, in which we expect a reduced genetic diversity compared to the diversity available in natural conditions.

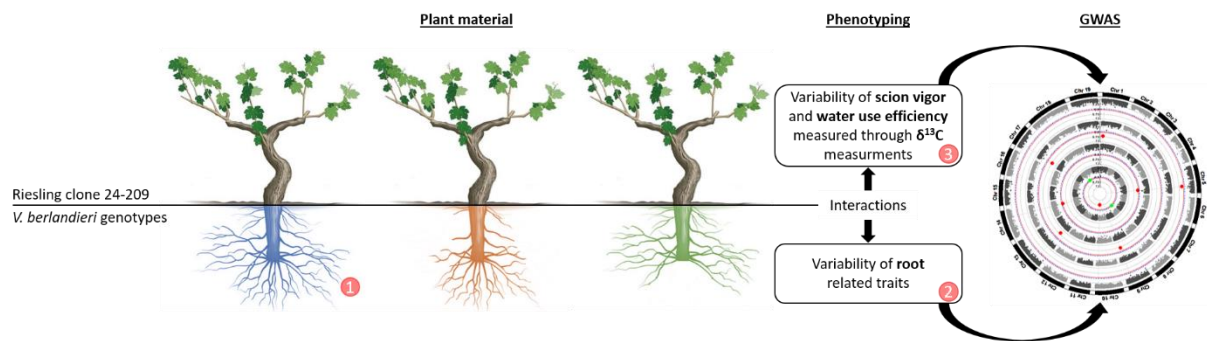
V. berlandieri hybrids have shown very good performances for rootstock selection criteria (vigor, phylloxera, water deficit, and limestone tolerance, Galet 1988) but the genetic bases of these traits have never been explored. The improvement of genetic association models allows control of the detection of false positive or negative signals. In addition, GWAS are not

carried out on progenies but directly on populations which make it possible to access to the association between the phenotypic and genetic variability in wild conditions.

In this context, this work aim to provide answers for several questions:

- Can we highlight a genetic structure in the wild *V. berlandieri* population?
- Does the phenotypic variability exist for root-related traits in the population at juvenile stage?
- Is it possible to detect genetic regions associated with root-related traits?
- What is the variability for conferred traits by the *V. berlandieri* rootstocks in a grafted context?
- Are root-related and conferred traits correlated?
- Can we detect genetic regions associated with the conferred traits variability?

The experimental strategy followed during the project (Figure 1.9) was to use a natural population of *V. berlandieri* grafted with one clone of Riesling and analyze the genetic structure of the population. The phenotype variability has been calculated for root-related traits and traits conferred to the scion. Then, the genetic architecture of these traits have been explored.



- 1 Chapter 3: Genetic structure and first genome-wide insights into the adaptation of a wild relative of grapevine, *Vitis berlandieri*
- 2 Chapter 4: Genome Wide Association for root related traits in a grafted wild *Vitis* population for rootstock breeding: *Vitis berlandieri*
- 3 Chapter 5: Association genetic of vigor conferred and $\delta^{13}\text{C}$ induced by grapevine rootstock: first study in a monospecies population of *Vitis berlandieri*

Figure 1.9 : Overall experimental strategy of the project. The main axis of the project are presented as chapters in the following document. Briefly, a natural population of *V. berlandieri* have been sampled and grafted with one clone of Riesling. The genetic structure of the population has been explored (1). Then phenotyping has been carried out for root-related trait (2) and the variability of traits conferred to the scion (3). Association mapping has been carried out in order to figure out association between the phenotype and the genetic levels.

Chapter 2: Project Materials and Methods

“Success is the ability to go from one failure to another with no loss of enthusiasm”

Winston Churchill

2.1 Plant material

2.1.1 *V. berlandieri* population origin

V. berlandieri species, considered as a *V. cinerea* sub-species is endemic from the Texas region (Galet 1988). Because of the agronomic performances (tolerance to water deficit and limestone) of hybrids issued from the *V. berlandieri* genetic background, a German and American team went through Texas, USA, in the Edward's plateau region and they ampelographically identified 86 female *V. berlandieri* (Schmid, Manty, and Cousins 2009). They harvested seeds of these plants after open-fertilization. After seedling and quality examination, 5,000 *V. berlandieri* genotypes were planted in field in Geisenheim, Germany. The genetic structure of the population of origin is presented in Chapter 3.

2.1.2 *V. berlandieri* sampling and grafting

Sampling

A sampling of the *V. berlandieri* gene-pool was used for the PhD project, because it was not possible to genotype and phenotype the entire population. Two criteria were used for this sampling step: first, in order to conserve the genetic diversity available in the field, three or four progeny genotypes per mother plant have been sampled; the second was to select genotypes showing good implantation in the field. Despite the bias introduced by this sampling method, the project was about rootstock breeding, thus it was meaningful to select higher potential genotypes.

Plants were sampled and grafted in 2019 and 2020 and we tried to obtain 5 repetitions per genotype. According to the grafting success, few genotypes were not present in the sampling and repetitions varied from 1 to 5 each year (Table 2.1). In this manuscript, because planting and measurements occurred the year after the grafting step, the sampling done in 2019 and 2020 are named Experiment1 and Experiment2 respectively.

Table 2.1 : Genotype repetitions in the population

	Experiment1	Experiment2
1 replicate	47	63
2 replicates	39	34
3 replicates	31	23
4 replicates	29	14
5 replicates	37	10
Total	183	144

In the final population, 211 genotypes were included of which 116 were common over the two years. Thus the number of replicates varied from 1 to 10 (Figure 2.1) leading to a population of 825 individuals.

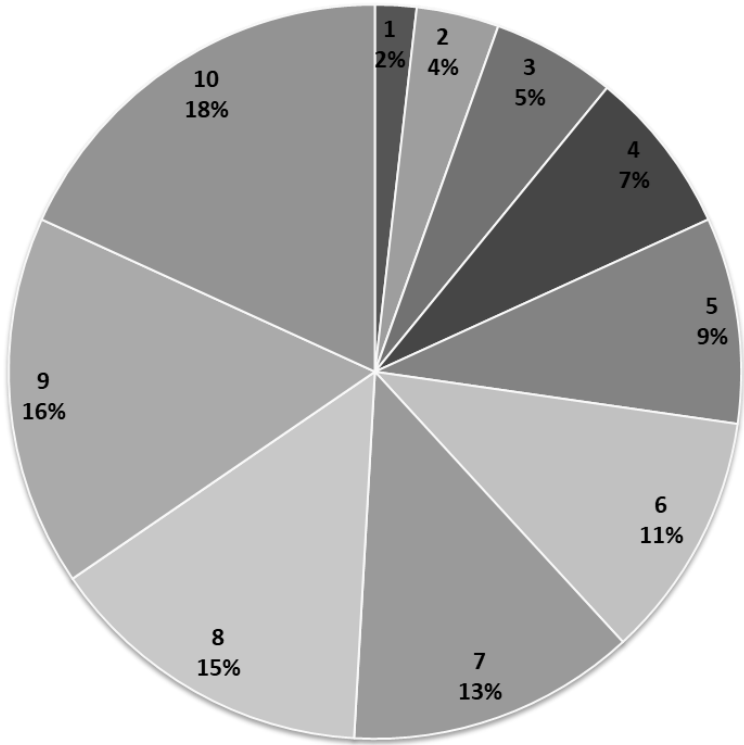


Figure 2.1: Number of genotypes replicates in the final population (2020/Experiment1 and 2021/Experiment2).

Grafting

Plants were grafted in the Grapevine Breeding institute of Geisenheim, Germany. Riesling scions were sampled at the end of January each year. In the field, each row was labelled with the scion:rootstock combination to avoid any mistake (Figure 2.2A). Shoots were pruned (Figure 2.2B) and cut into small wood pieces (Figure 2.2C), all diameter were conserved in order to optimize the diameter association between scions and rootstocks during grafting. At this step, the scion corresponds to a small piece of wood (4cm to 7cm) constituted by one node and one bud. One or two centimeters are conserved on the upper part to avoid desiccation and few centimeters on the lower part for grafting. Woody material was treated with Beltanol solution in order to keep the material free of microorganisms (Figure 2.2D) and stored in plastic bags (Figure 2.2E) in wet conditions in cold rooms.



Figure 2.2 : Wood sampling process of Riesling clone 24-209 before grafting. Rootstock :scion combinations are organized by row in fields (A). Shoot have been pruned (B) and allowed us to obtain various scion diameter (C) keeping one nod for grafting. Pieces of wood were treated with beltanol solution (D) to avoid microorganisms proliferation. Wood material have been stored in bags (E) in a cold room.

Later on (February/March) the *V. berlandieri* sampling was made. To do so, all genotypes selected for the project were labelled in the field in order to avoid any mistake (Figure 2.3A and B). Shoots were pruned (Figure 2.3C) and cut in pieces of wood of 25cm (Figure 2.3D). Two or three nodes were conserved by sample and all buds were removed (Figure 2.3E) in order to favor the grafting union. All piece of wood from the same genotype were bundled (Figure 2.3F and G) and maintained in wet conditions (Figure 2.3H) before Beltanol treatment and storage in cold room (3°C).



Figure 2.3 : V. berlandieri sampling process for grafting. All plants were labelled (A) to avoid mistakes in field (B). Shoots were pruned (C) and the labels were conserved during the whole process of sampling (D). Buds were removed from the piece of wood (E, before removing upside and after removing downside). Woody material was bundled by genotype (F) and by field (G) and maintained in wet conditions (H).

Grafting was made mechanically with omega grafting technic in March. Plants were grown in warm room (Figure 2.4A) for one month. After the first leaves appeared (Figure 2.4B), plants were grown in plastic boxes filled with a mix of earth and peat (Figure 2.4C). Then plants were evaluated for their quality, including shoot growth, root growth, and grafting point solidity. Plants with a correct quality (grafting success) were individually potted (Figure 2.4D) and grown with no limiting conditions until November (leaves fall period).



Figure 2.4 : Growth of grafted plants. After grafting plants were grown in a warm room (A) until the first leaves appeared (B). They were boxed with potting soil in a greenhouse (C) and individuals with a correct grafting quality (root and shoot growth started and a solid grafting point) were potted and grown in a greenhouse (D).

2.2 Genotyping by sequencing data

2.2.1 Sampling

The sampling for sequencing was made between the 28th of June and the 4th of July. The description of sampling is presented in chapter 3. To summarize it, two leaf disc were sampled on young leaves per genotype (Figure 2.5A). During the sampling, samples were stored in cold conditions (Figure 2.5B), and freeze dried (Figure 2.5C). Samples were stored in 96 deep well plates until the library preparation.



Figure 2.5 : Sampling for sequencing. Two leaf discs were sampled by genotype (A), conserved in cold conditions during the sampling, and freeze dried (C).

2.2.2 Libraries preparation and sequencing

The libraries preparation was done with the genotyping platform of the UMR AGAP, CIRAD, Montpellier, France. Sequencing data processing was conducted with the Bioinfo Genotoul platform (GenoToul Bioinfo 2018). The details of the sequencing are presented in chapter 3.

2.3 Experimental field design

2.3.1 The *V. berlandieri* population of the Grapevine Breeding Institut in Geisenheim, Germany

The *V. berlandieri* population is planted in field in the Grapevine Breeding Institut in Geisenheim, Germany. In total 5,000 genotypes were planted ungrafted in field in 2005 and spread into three plots (Figure 2.6).

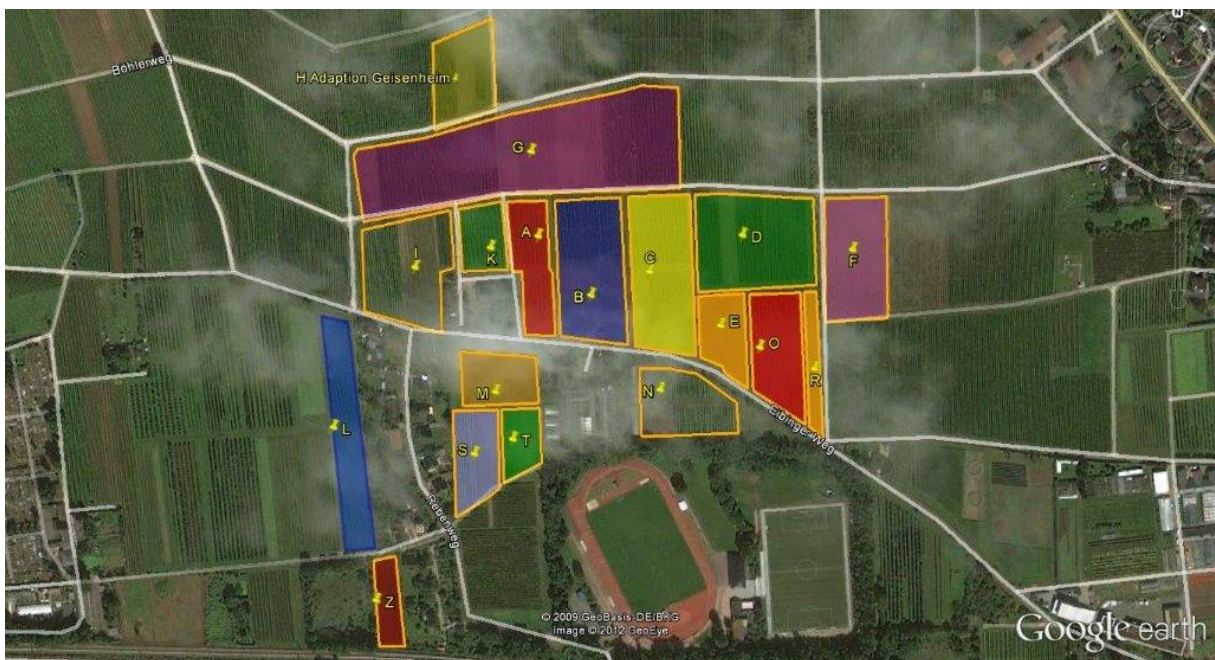


Figure 2.6: Field organization in the Department of Grapevine Breeding of the Hochschule Geisenheim University. The gene-pool used in the project is spread in fields I, S, and Z.

2.3.2 The *V. berlandieri* population of the PhD project

The second location was in Villenave d'Ornon next to the ISVV (Institut des Sciences de la Vigne et du Vin) building. The grafted genotypes were planted and grown in field in 2020 and 2021. Based on the resistivity map of the field (Figure 2.7A), plants were placed in five different blocks in 2020 (Figure 2.7B). In 2021, the number of genotypes and repetitions were lower than in 2020, then all plants were only separated into two blocks (Figure 2.7B) in order to avoid obtaining unbalanced group sizes during the data statistical processing.

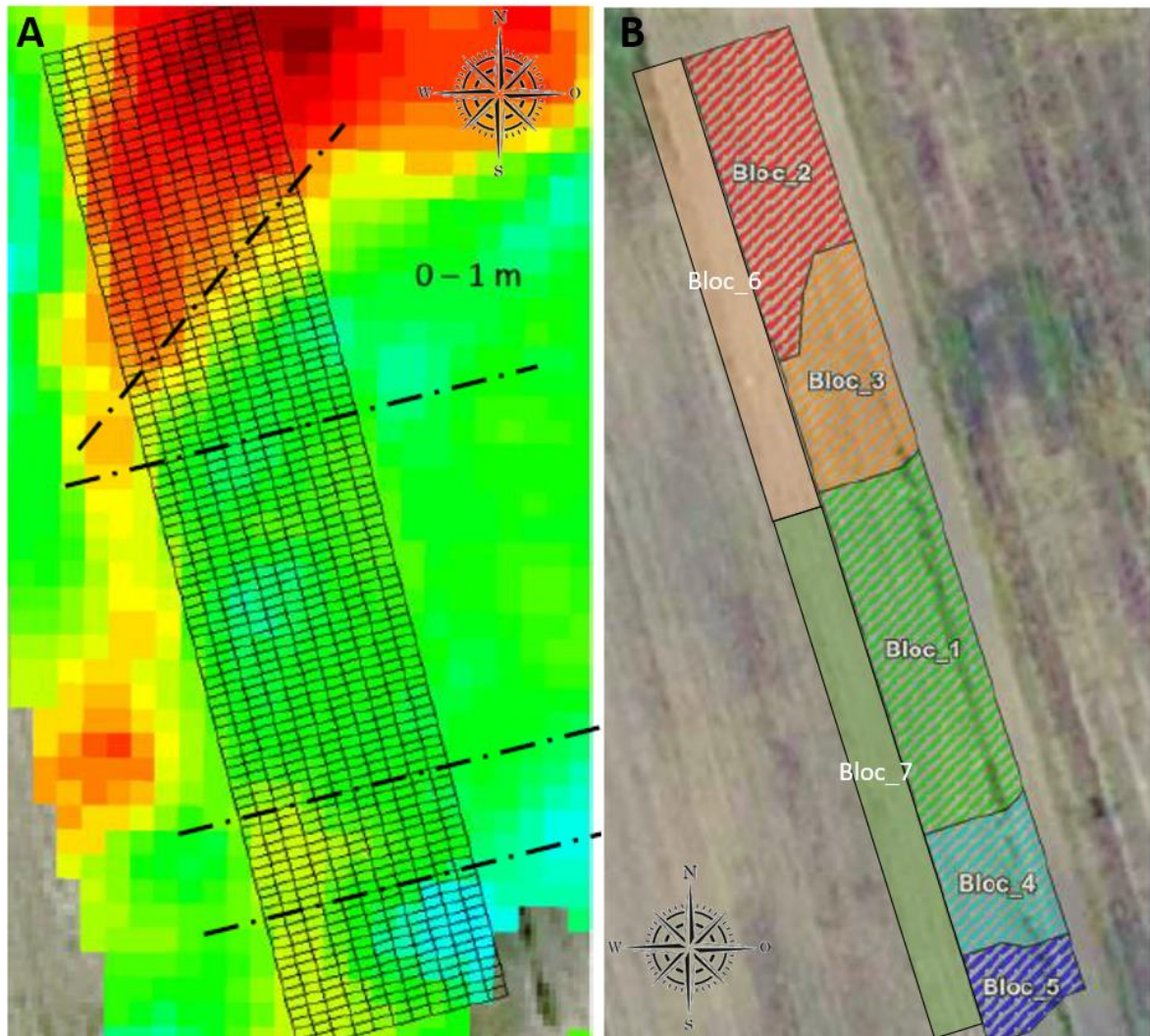


Figure 2.7: Experimental field in Villenave d'Ornon, France. The resistivity map (A) indicates the soil resistivity, vertical lines indicate rows and vertical ones indicate plant position. The dashed lines indicate the partitioning of the field in blocks. The blocks (B) are indicated for the 2020 planting (Bloc_1 to Bloc_5) and 2021 (Bloc_6 and Bloc_7).

2.4 Phenotyping

2.4.1 Root phenotyping

After 8 months of growing with out limiting conditions, plants were potted out, shoots were pruned, and the root systems were washed with pressurized water. Plants were stored in cold rooms after a Beltanol treatment in order to avoid fungi development during storage.

Root systems were pruned 4cm below the collar and all primary roots were counted and each diameter was measured with a semi-automatic caliper. Roots were conserved in order to obtain the root dry weight. Roots were divided into classes according to their diameter in *small* roots (diameter < 1 mm), *medium* roots (1 mm > diameter < 2 mm) and *large* roots (diameter > 2 mm). This allowed us to analyze 10 root-related traits over the two years of experiment: the root dry weight (RDW), the average diameter (Av_Diam), the total diameter (Tot_Diam), the total number of roots (Tot_Root_NB), the number of *small*, *medium*, and *large* roots (NB_Small, NB_Medium, and NB_Large), and the proportion of each class of roots (Prop_Small, Prop_Medium and Prop_Large). After root and shoot pruning, plants were weighed in order to observe differences in the weight of the woody part of the plant and then analyze its impact on root development. During the root phenotyping of the second year, the root maximal length was measured. However, because this trait was only available for one year, it has not been used in analyzed.

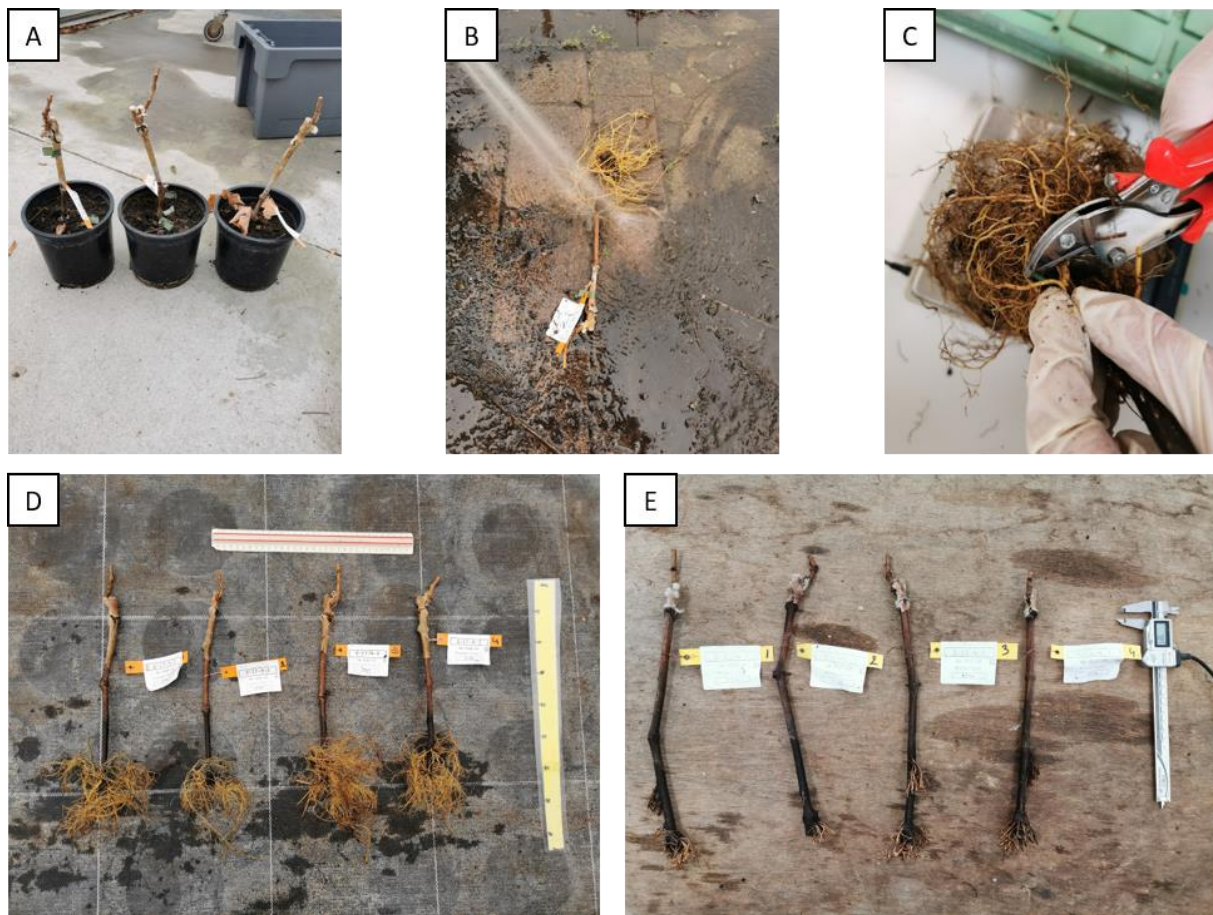


Figure 2.8 : Root phenotyping process. Plant are pruned (A), potted out and washed with pressurized water (B). Root are pruned 4cm after the collar (C). Before root phenotyping, the root system architecture diversity was observed between individuals from the same genotype (D). After root phenotyping, all plants were ready to be sent in France (E).

After root phenotyping, plants were stored in cold room in wet conditions and sent in Bordeaux, France to be planted in field.

2.4.2 Scion phenotyping

Measurements on the scion part of the plant occurred in France in the field experiment. The vigor was measured by cutting the shoots at the end of the winter period in order to obtain the pruning weight (PW) of each genotype.

Each year, several predawn water potentials were measured in order to use it as an indicator of the water status of the plants in the field. Moreover, the number of leaves was counted every 2-3 weeks in order to know which leaf appeared during a period of 2-3 weeks on each plant. Then it allowed us to select the best period in term of climate and sample a leaf appeared during this period for $\delta^{13}\text{C}$ analyses (the end of August in 2020 and the start of August in 2021). The $\delta^{13}\text{C}$ was analyzed for all plants over the three years of experiment.

Because we were in field condition, the water status of plants depended on climate variation during the vegetative period (April to October). Accordingly, no water deficit was experienced by the plants during 2020 and 2021. However, the summer 2022 was very hot and dry which allowed us to observe water deficit symptoms on plants (leaves fall, stop growth and predawn water potentials of moderate water deficit conditions). Two measurements were done in 2022 before and during the water deficit event in order to compare the impact of *V. berlandieri* rootstocks genotypes on the water use efficiency behavior of the Riesling scions.

2.5 Statistical process

2.5.1 Descriptive statistics

During the PhD project, all data were analyzed thanks to R (R Core Team, 2021). Graphics were constructed with the `ggplot2` package (v3.3.3; Wickham, 2016) and the `dplyr` package (Wickham et al., 2018) have been very helpful for data handling. PCA were constructed using the `FactoMineR` package.

2.5.2 Statistical models BLUP and BLUE handling

The H^2 extracted from variance-covariance matrix issued from mixed models. In these models, the genotype was considered as random effect (allowing us to access the variance-covariance matrix) and other factors were considered as fixed effect in order to sort out the variance due to genetics from the variance explained by external factors. These models were BLUP models which was predictive and widely used in animal breeding. These models were pessimistic reducing the general variance between genotypes, therefore predictive values were not used for next analyses.

The genetic values used in GWAS were obtained by using the same model as in BLUP but considering genotypes as fixed effect in generalized linear models which were BLUE. The estimate of each genotype was considered as the genetic value of the genotype for the trait of interest and used in GWAS.

Models were constructed using two R packages `lme4` and `lmerTest`. GWAS were done with `Gapit` on R. Details are indicated in respective chapters.

Chapter 3: Genetic structure and first genome-wide insights into the adaptation of a wild relative of grapevine, *Vitis berlandieri*

“Genius is one percent inspiration and ninety-nine percent perspiration”

Thomas Edison

Introduction

This chapter submitted to *Evolutionary Applications* journal aims to highlight the genetic structure of the *V. berlandieri* population. Because the population structure can strongly impact GWAS results (Pritchard, Stephens, and Donnelly 2000), we analyzed it before starting any association study. The population was expected to be structured by kinship relationship between genotypes (unrelated, half-sibs, full-sibs...). Moreover, according to the sampling location of wild vines in Texas, isolation by distance (IBD) and variations in environmental conditions could also impact the genetic structure of the population. Thus, to characterize the environmental conditions in which each subpopulation have been found, climatic parameters were extracted from the TerraClimate platform (Abatzoglou et al. 2018). Then, associations between the genetic and environmental variability have been explored using a genome-environment association (GEA) method.

Genetic structure and first genome-wide insights into the adaptation of a wild relative of grapevine, *Vitis berlandieri*

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3.1 Abstract

In grafted plants, such as grapevine, increasing the diversity of rootstocks available to growers is an ideal strategy for helping plants to adapt to climate change. The rootstocks used for grapevine are hybrids of various American *Vitis*, including *V. berlandieri*. The rootstocks currently in use in vineyards are derived from breeding programs involving very small numbers of parental individuals. We investigated the structure of a natural population of *V. berlandieri* and the association of genetic diversity with environmental variables. In this study, we collected seeds from 78 wild *V. berlandieri* plants in Texas after open fertilization. We genotyped 286 individuals to describe the structure of the population, and environmental information collected at the sampling site made it possible to perform genome-environment association analysis (GEA). *De novo long-read whole-genome sequencing was performed on V. berlandieri* and a STRUCTURE analysis was performed. We identified and filtered 104378 SNPs. We found that there were two subpopulations associated with differences in elevation, temperature and rainfall between sampling sites. GEA identified three QTL for elevation and 15 QTL for PCA coordinates based on environmental parameter variability. This original study is the first GEA study to be performed on a population of grapevines sampled in natural

conditions. Our results shed new light on rootstock genetics and could open up possibilities for introducing greater diversity into genetic improvement programs for grapevine rootstocks.

Key words: Grapevine, Rootstock, Population genetics, Genome-wide association, Genotyping by sequencing, Whole-genome sequencing, Long reads

3.2 Introduction

In the context of climate change, the resilience of plants in natural populations and the productivity of agronomic species are compromised (Parmesan and Yohe 2003; Root et al. 2003). The increasing frequency and intensity of threats such as drought, nutrient shortages and the arrival of new pests and pathogens are introducing new challenges into plant breeding programs, which are increasingly called upon to develop new varieties able to overcome these environmental pressures.

Natural selection has tested a much wider range of gene combinations under various environmental pressures than could ever be tested in plant breeding programs (Cortés and López-Hernández 2021). For this reason, studies of the genetic basis of the adaptation of wild relatives of cultivated species to their native environments can provide useful genetic potential for incorporation into breeding programs (Condon et al. 2004; Vadez et al. 2014).

In recent years, improvements in sequencing technologies have made deeper explorations of the genetic basis of phenotype variability possible. Genome-wide quantitative genetic studies can identify markers associated with traits of interest. Following their identification and validation, these quantitative trait loci (QTL) can be used in marker-assisted selection (MAS; Tuberosa et al. 2007) to improve agronomic traits with a simple genetic architecture in crop plants; this approach has been used to increase yield in maize, rice, barley and soybean (Francia et al. 2005). Genome-wide association studies (GWAS) are based on the combination of ancestral recombination events (Nordborg and Tavaré 2002) and information about linkage disequilibrium (LD); they can be used to detect associations between allelic and phenotypic variation. This approach makes it possible to hone in on the positions of loci controlling traits

of interest by making use of the large number of recombination events that have occurred over many generations in natural populations. The main limitation of GWAS has been the extent of LD, which can be affected by many factors, including structuring of the population, population size, and genetic drift (Remington et al. 2001), leading to high false discovery rates and inconsistent results. Population structure and kinship are two major confounding factors in the detection of genotype-phenotype associations (Kang et al. 2008; 2010; Zhang et al. 2010; Santure and Garant 2018). However, it is possible to control for the false discovery rate in current statistical models without increasing computing time by considering kinship, structure, and LD (Huang et al. 2018).

A particular case of GWAS uses environmental variables instead of phenotypes to identify a link between genetics and environment (genome-environment association, GEA) in wild populations (Santure and Garant 2018). This makes it possible to explore the genetic basis of adaptation to the environment, and to identify loci with allele frequencies correlated with climatic data (Bragg et al. 2015). GEA studies are complementary to GWAS, as they can reveal adaptive patterns that are difficult to detect with GWAS approaches, and can identify the major environmental forces behind natural selection (Rellstab et al. 2015). Approaches of this type have been applied to the wild relatives of several crops, including barley (Abebe, Naz, and Léon 2015), as a means of identifying putative adaptive loci and selecting gene pools adapted to specific environmental conditions. In perennial species, such as trees, GEA has been successfully used to identify populations displaying potential preadaptation to the predicted future climate (Pluess et al. 2016; De La Torre, Wilhite, and Neale 2019). It could ultimately be used in the development of genetic markers to assist breeding strategies and to facilitate the precise selection of new wild genotypes for inclusion in breeding programs (Cortés, López-Hernández, and Blair 2022).

The genetic load of breeding populations has also been identified as one of the main challenges in the transition to next-generation breeding (Wallace, Rodgers-Melnick, and Buckler 2018). According to population genetics theory, most of the new mutations occurring in a population are neutral or slightly deleterious (Ohta 1973; Kimura 1983). Mutations with a strong deleterious effect should be rapidly eliminated by purifying selection. However, the efficacy of purifying selection for removing harmful alleles may be compromised in certain

situations, such as demographic bottlenecks (González-Martínez, Ridout, and Pannell 2017; Peischl et al. 2013), and in the presence of Hill-Robertson interference (i.e. a phenomenon that links alleles with potentially different fitness values in regions of low recombination) (Hill and Robertson 1966). Decreases in the efficacy of purifying selection lead to the accumulation of deleterious mutations that may compromise the fitness of natural populations or the productivity and resilience of crop species. The identification, control and repair of such mutations in major crop species is, therefore, crucial for the persistence of natural populations and for breeding programs.

Grapevine (*Vitis vinifera*) breeding programs are particularly challenging because this perennial plant species has been grafted onto rootstocks since the phylloxera crisis in the 19th century. *Vitis vinifera* is used as the scion, to maintain grape yield and quality, but other *Vitis* species resistant to phylloxera are used as rootstocks. These rootstocks are derived from hybridizations between American species (mostly *V. riparia*, *V. rupestris*, and *V. berlandieri*) and sometimes with *V. vinifera* (Galet 1988). Their selection for use in vineyards is based on their tolerance to phylloxera, chlorosis and water deficit tolerance, and the vigor conferred. Several studies have investigated genetic structure in grapevine (Aradhya et al. 2003; Arroyo-García et al. 2006; Frenkel et al. 2012; Myles et al. 2010; 2011; Laucou et al. 2011; 2018; Cipriani et al. 2010; Grassi et al. 2003; Imazio et al. 2006; Péros et al. 2021; 2015; 2011), but such studies have never been performed in a specific American *Vitis* genetic background. Rootstock identification is traditionally based on ampelographic traits (Galet 1956; Ravaz 1902) and genetic studies have essentially been restricted to *Vitis vinifera*, with little effort devoted to grapevine rootstock genetics (Andrés et al. 2007; Arroyo-García et al. 2006; Myles et al. 2011; Bianchi et al. 2020; Péros et al. 2011; 2015; 2021). New crosses are being performed to develop additional grapevine rootstocks, but mostly with the genotypes available in germplasm collections, and very little exploration of the genetic diversity existing in natural conditions (Summaira Riaz et al. 2019). However, one recent study (Péros et al. 2021) based on SSR and SNP markers revealed a high level of genetic diversity in 421 genotypes of *V. aestivalis*, *V. cinerea* (var. *berlandieri* and *cinerea*) and *V. riparia*.

V. berlandieri is commonly used in crosses for the development of new grapevine rootstocks. Its hybrids perform well, but are difficult to use, mostly due to poor root emission after grafting (Boubals 1966; Galet 1988). However, the *V. berlandieri* genetic background is

involved in hybridization to produce a number of widely used grapevine rootstocks, such as 110 Richter (*Vitis berlandieri* cv. Rösséguier no. 2 x *Vitis rupestris* cv. Martin), Fercal (Berlandieri Colombard no. 1 B x 31 Richter), Gravesac (161-49 Couderc x 3309 Couderc) and SO4 (*Vitis berlandieri* x *Vitis riparia*). The *V. berlandieri* genotypes used for hybrid creation were selected rapidly at the start of the 20th century on the basis of surveys performed across the USA. Unfortunately, this genetic background has never been explored more deeply, and the diversity and genetic architecture of traits of interest in *V. berlandieri* in the wild remains unknown. This species is endemic to the Edwards Plateau area in Texas (USA), a dry, chalky region (Schmid, Manty, and Cousins 2009). In a previous study on American genetic backgrounds, *V. berlandieri*, which is considered to belong to the *V. cinerea* subgroup, was clearly separated from other groups (Péros et al. 2021). However, the genetic background of wild *Vitis* has not yet been explored. In this study, we addressed the following objectives: i) characterization of the genetic structure of *V. berlandieri*; we generated genome-wide molecular markers from a *de novo* assembly of the *V. berlandieri* genome for this purpose; ii) exploration of the genomic features of this species in terms of the extent of linkage disequilibrium and genetic diversity and their variation according to genetic structure; iii) study of deleterious allele accumulation in the different subpopulations; and iv) identification of genes potentially involved in the adaptation of this species to the environment.

3.3 Materials and Methods

Plant material

In 2005, 78 wild female *V. berlandieri* plants were ampelographically identified in Edwards Plateau (transect of 40,000 km²; from N 31°23' W 100°2' to N 29°43' W 97°26') in Texas, USA. The coordinates and elevation of each sampling site were recorded. We harvested approximately 40,000 seeds from these plants after open fertilization, and about 5,000 of these seeds were sown in a field at Geisenheim University, Germany. We selected 286 genotypes within this population on the basis of vigor, such that each initial “mother” plant was represented by four genotypes (half-sibs) to encompass the available genetic diversity.

Reference genome

The reference genotype for this study was ‘*V. berlandieri* 10585’ (NCBI, BioProject ID:

PRJNA886625) from the collection of INRAE-Bordeaux, (Villenave d'Ornon, France). This genotype was selected on the basis of its rooting capacity and use in other experiments. 'V. berlandieri 10585' leaves were harvested from the INRAE Bordeaux grapevine collection (Villenave d'Ornon, France). Two young leaves with a width of about 5 cm were collected, frozen and stored in a -80°C freezer for DNA extraction. DNA was extracted with the Tip 100 Qiagen Genomic kit, according to a slightly modified version of the manufacturer's protocol. We incubated 0.5 g of ground plant material with 9.5 mL of G2 buffer supplemented with 1% PVP-40, 19 µL RNase A and 500 µL proteinase K for 3 hours at 50°C for lysis. The lysate was subjected to tip filtration and the DNA was precipitated with isopropanol, centrifuged for 15 min at 5000 x g, washed with 70% ethanol and resuspended in 50 µL TE buffer. The quality and molecular weight of the DNA isolated were checked. An A_{260}/A_{280} ratio between 1.8 and 2.0 and an A_{260}/A_{230} ratio between 2.0 and 2.2 were obtained, and an Agilent Genomic DNA Screentape analysis was performed. We used 10 µg of high-quality DNA for sequencing. Samples were sequenced with Single-Molecule Real-Time PACBIO SEQUEL II HIFI long reads at the INRAE Clermont-Ferrand GENTYANE platform (France).

DNA consensus call sequences obtained in BAM format were converted to Fastq format with the bam2fastq tool from the SMRTLink v11.0 PACBIO library. The HIFI sequencing DNA quality was checked with FastQC version 0.11.7. Paternal and maternal kmers were identified with yak-0.1 software, using the parental reads. The outputs were then used in hifiasm-v0.15.5 to bin long reads and to assemble the two haplotypes. For each haplotype, contigs were aligned with PN40024.v4 with minimap2 version 2.17. The best contig alignments were used to build an AGP file, and each pseudomolecule was then reconstructed. We refined the pseudomolecules by repeating the process, beginning with an alignment of each haplotype against the other, previously reconstructed haplotype. The embryophyta_odb10 lineage package from BUSCO 5.3.1 software was used in genome mode to estimate the completeness of all assemblies.

Genotyping by sequencing

Leaves were sampled from all 286 genotypes at Geisenheim University, Germany. Two leaf discs of 1.5 cm diameter were sampled from each genotype and placed on ice. The leaf discs were then frozen in liquid nitrogen and freeze-dried in a Martin Christ, Beta 2-8LD freeze-dryer. DNA was extracted from all lyophilized samples as described by Cormier et al. (2019) in

Corning/Costar deep 96-well 1.1 mL plates. Libraries were prepared at UMR AGAP, CIRAD (Montpellier, France) as described by Elshire et al. (2011). Based on our results, the amount of DNA was normalized to 50 ng/mL. We prepared 96-plex GBS banks with the restriction enzyme ApeKI. Illumina Hiseq 4000 short-read 2 × 150 bp sequencing was performed by Genewiz (Montpellier, France). Three 96-plex plates were used. The raw data are available on NCBI, BioProject ID: PRJNA886619.

SNP calling

GBS data were processed with the Genotoul cluster, Toulouse, France. Reads were demultiplexed with a script available from <https://github.com/timflutre/demultiplex.py> and cleaned with Cutadapt (Martin 2011) with filters “-a AGATCGGAAGAGCGGTTCAGCAGGAATGCCGAG -A GAGATCGGAAGAGCGTCGTGTAGGGAAAGAGTGT -G CTCGGCATTCTGCTGAACCGCTCTCCGATCT -g ACACTCTTCCCTACACGACGCTCTCCGATCT -u 7 -U 7 -m 17”. Sequences were aligned with the *V. berlandieri* reference genome obtained in this study. VCFs were joined with GATK tools (McKenna et al. 2010), and 3,294,984 SNPs were obtained. SNPs were filtered, with the rejection of SNPs with a quality depth < 2.0, Fisher strand value > 60.0, MQ < 40.0, MRankSum < -12.5 and ReadPosRankSum < - 8.0. These filters were applied one by one, as recommended in the GATK support documentation. In total, 3,294,747 SNPs were conserved and individuals with more than 80% missing data were filtered out ($n=281$ genotypes retained). VCFtools (Danecek et al. 2011) was used for filtering based on the following criteria: minimum depth of 3, maximum of 50% missing data, minor allele frequency of 0.05 and a minimum mean depth of 5. In total, 104,378 SNPs were conserved. We considered 281 genotypes with less than 60% missing data.

Population structure

Two methods were used for the analysis of population structure. We first ran STRUCTURE v2.3.4 (Pritchard, Stephens, and Donnelly 2000) on all 104,378 SNPs. The optimal number of subpopulations was determined as previously described (Evanno, Regnaut, and Goudet 2005). One to 10 populations were allowed, with a burn-in period of 20,000 and a Markov Chain-Monte Carlo (MCMC) iteration number of 20,000 without prior knowledge of population affinities and three runs. The optimal number of populations was found to be two ($K=2$). A

new run was then performed, with a burn-in period of 100,000 and 100,000 MCMC iterations. Genotypes with a membership proportion greater than 0.8 for a population were attributed to the population concerned. Genotypes not attributed to a particular population were considered to be admixed. The STRUCTURE results were then compared with those of a *k*-means clustering method described elsewhere (Voss-Fels et al. 2015). A genetic matrix distance was calculated with Roger's distance (RD). Clusters were identified by the unweighted-pair-group with arithmetic mean (UPGMA) method, based on Roger's genetic distance. Genotypes were then attributed to a cluster by the *k*-means clustering method, with the Hartigan and Wong algorithm (1979). The optimal number of clusters was determined by plotting cluster numbers from 1 to 15 against the corresponding within-cluster sum of squares (Voss-Fels et al. 2015). This calculation was performed 20 times and the mean value of each run was reported. The optimal number of clusters was found, by eye, to be $K=5$, as beyond this value, increasing the number of clusters did not significantly decrease the within-cluster sum of squares. The results were visualized by plotting PCA results constructed with the first four principal components according to marker information. The number of clusters in the PCA was chosen based on the optimal K value from STRUCTURE analysis considering admixed individuals as a subpopulation ($K=3$) and from the visualization of within-cluster sums of squares ($K=5$).

We tested for isolation by distance by calculating Nei's distance matrix between genotypes with the *adegenet* package in R. As there were several genotypes originating from each mother plant, the mean genetic distance was calculated between mother plants so as to obtain a single value for the genetic distance between two mother plants. A distance matrix was constructed from the GPS coordinates of the mother plants with the *sp* package in R. A Mantel correlation test was performed by the Spearman method, with 9,999 permutations.

Linkage disequilibrium, genetic diversity and genetic load

Linkage disequilibrium decay was estimated as the physical distance at which r^2 reached a value of 0.2, as previously described (Hill and Weir 1988). Intrapopulation F_{ST} was calculated by STRUCTURE and interpopulation ($K=2$) F_{ST} was calculated with VCFtools (--weir-fst-pop option), using the default parameters. Hardy Weinberg equilibrium (HWE), Tajima's D and allelic diversity (π) were calculated for the entire population and by subpopulation ($K=2$). After VCFtools filtering, 102,394 SNPs were considered for the exploration of HWE. HWE and π were

calculated for each SNP. Tajima's D was calculated with a 10 kb sliding window. All the parameters were obtained with VCFtools-0.1.15 (Danecek et al. 2011) implemented on the Genotoul cluster. Only one genotype per mother plant was retained in each group, to prevent genetic shrinkage in the calculation of HWE and Tajima's D. SnpEff (Cingolani et al. 2012) was used to attribute a potential impact to each SNP according to its position in the DNA sequence. The *V. berlandieri* reference genome was annotated according to the Pinot noir reference genome (12X.v2; Canaguier et al. 2017), with liftoff1.6.1. In total 39,250 of the 42,413 genes from the Pinot noir reference genome (92.5%) were found in *V. berlandieri*. The annotated *V. berlandieri* genome was added to the program as an additional reference genome. SnpEff was run with default parameters, and two items of information were considered in our analyses: the predicted impact of the SNP on the DNA sequence and the effect of the SNP according to its location in the genome (see Supplementary Table S2 for a detailed list of effects). Impacts were classified into four categories: "high" (e.g., loss of function of the protein), "moderate" (e.g. modification of protein efficacy), "low" (probably no impact on protein) and "modifier" (mostly non-coding variants or variants for which there was no evidence of impact). Kimura's neutral theory of evolution (Kimura 1968) suggests that most mutations are deleterious or neutral. We therefore calculated the genetic load as follows:

$$P_{del} = \frac{\text{Number of derived alleles not similar to the reference genome for "high" impact SNP}}{\text{Number of alleles for SNP with "low","moderate" and "high" impact} \times 2} \quad (1)$$

This equation (1) considers " P_{del} " as the proportion of deleterious alleles for one individual. SNPs with missing data were not considered for each individual. The accumulation of deleterious alleles in each population was evaluated as the mean P_{del} of the individuals assigned to each population according to STRUCTURE analysis divided by the number of deleterious alleles for all individuals from each population. For each SNP, snpEff could propose several impacts and effects. In such cases, we retained the first effect/impact proposed by the program, which was the most deleterious.

Genome-wide association with environmental variables

Genome-environment association (GEA) analysis was performed with the elevation of the mother plants reported during sample and additional environmental information extracted from the TerraClimate platform (Abatzoglou et al. 2018) for each of the mother plant

coordinates. The following environmental parameters were obtained for the 1991-2020 period, at a resolution of 4 km:

- Growing season temperature (GST, from April to October, Jones 2006) and growing season temperature during the vegetative period (GST49, between April and September). The mean daily average temperature is calculated over the period concerned. This parameter affects earliness and grape quality (Jones *et al.*, 2006).

- Growing season rainfall (GSR from April to October, Bois, Zito, and Calonnec 2017) and growing season rainfall during the vegetative period (GSR49, from April to September). This parameter is calculated as the cumulative amount of rainfall (mm) over the period concerned. It provides a rough estimate of the amount of water available to the plant during the corresponding period.

- Springtime rainfall (RRSPR), which is essentially GSR for the period between April and July. It can be used as an indicator of biotic pressure during the first few months of vegetative growth (Bois, Zito, and Calonnec 2017).

- Branas hydrothermal index (HYB; Branas, Bernon, and Levadoux 1946), which evaluates the risk of grapevine exposure to disease.

- Winter freeze risk index (WFR; Bois, Moriondo, and Jones 2014) is the mean minimum temperature in January. If this temperature is $>4^{\circ}\text{C}$, the risk is considered to be low, whereas the risk is considered high if it is $<-11^{\circ}\text{C}$.

- Spring frost risk index (SFR; Bois, Moriondo, and Jones 2014) is the mean minimum temperature in April. The risk is considered low if this temperature is $>12^{\circ}\text{C}$ and high if it is $<0^{\circ}\text{C}$.

- Heat stress index (HST; Bois, Moriondo, and Jones 2014) is the mean maximum temperature in July. The risk is considered to be low if this temperature is $<25^{\circ}\text{C}$ and high if it is $>30^{\circ}\text{C}$.

- The Huglin index (HI; Tonietto and Carbonneau 2004) provides information about the climate of the region. It combines mean air temperature (T , $^{\circ}\text{C}$), the maximum air temperature (T_x , $^{\circ}\text{C}$) and day length coefficient (d) according to latitude, between April and September. This

parameter may reflect the sugar-producing potential of the plant during the vegetative period in a given context.

$$Hi = \sum_{01/04}^{30/09} \frac{(T - 10) + (Tx - 10)}{2} d$$

- Cool night index (CI, Tonietto and Carbonneau 2004) is the mean daily minimum air temperature in September. It provides qualitative information about the potential of wine-producing regions based principally on the production of secondary metabolites (polyphenols, aromas).

- Dryness index (DI, Tonietto and Carbonneau 2004) is an indicator of potential soil water availability according to the dryness of a climatic region. It is adapted from the soil index of Riou (Riou *et al.*, 1994) and it affects ripening and wine quality (Carbonneau, 1998).

The Pearson coefficients of correlation between these environmental variables were explored. GST and GST49 were highly correlated, as were GSR and GSR49 (coefficients of 0.99 for both). We therefore included only GST49 and GSR49 in the PCA calculation. A GEA analysis was performed for elevation, and then for the first two principal components of the PCA performed with TerraClimate environmental parameters. Elevation was analyzed separately from the other environmental parameters because it was measured during the sampling campaign, whereas the other environmental variables were obtained by climatic interpolation.

We performed GEA with the BLINK model in GAPIT with default settings, implementation by major allele and MAF>0.05 filtration. The BLINK model was used because of the ease with which false discovery rate can be controlled in this model (Huang et al. 2018). The information about population structure obtained from STRUCTURE (K=2) was used as a covariate. In this model, kinship was derived from pseudo-QTN information. Bonferroni correction was applied to the calculated *p*-values. The significance thresholds were, thus, set at 0.05/*n* and 0.01/*n* where “*n*” is the number of markers used. The GEA analysis was performed on the 281 genotypes with 88804 SNPs after the recalculation of minor allele frequency in GAPIT.

The genes attributed to each marker by snpEff were used to identify the related protein families with the UniProtKB (The UniProt Consortium 2021) database. If several results were available, only one was retained. If the corresponding protein was unknown, we used the molecular function attributed by IEA:InterPro (Camon et al. 2005) or the manual assertion based on the work of Gaudet et al. (2011).

3.4 Results

The long-read sequencing of *V. berlandieri* resulted in 91% of reads having a length between 10 kb and 20 kb; 10 chromosomes presented a single contig, eight chromosomes had two contigs and one chromosome was divided into three contigs. This high-quality assembly resulted in a highly reliable reference genome for these analyses.

Population structure

The optimal number of subpopulations determined by STRUCTURE was $K=2$ according to the method of Evanno, Regnaut, and Goudet (2005) (burn-in = 20,000 and no. of MCMC iterations = 20,000). The two subpopulations were explored in greater depth (burn-in = 100,000 and no. of MCMC iterations = 100,000) (Figure 3.1A); subpopulation 1 was found to contain 100 genotypes, subpopulation 2 contained 63 genotypes, and the admixed subpopulation contained 118 genotypes.

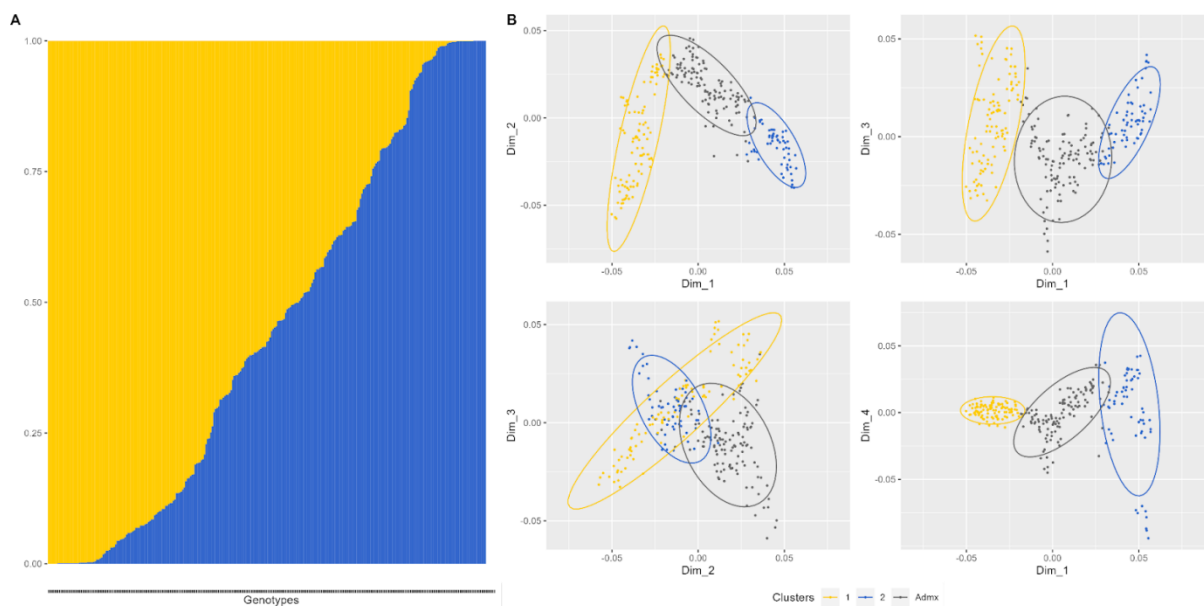


Figure 3.1 : Population structure results from (A) STRUCTURE $K=2$. The proportion of each genotype found in the two populations is shown. Whenever a genotype has a probability of belonging to a population of 80% or more, the genotype is attributed to that population. (B) PCA based on SNP information, the first principal components are represented and all genotypes are plotted and colored according to STRUCTURE groups ; PC 1 to 4 explained 4%, 2%, 2%, and 1% of the variability, respectively.

The *k*-means clustering method suggested that there were more subdivisions within the population, resulting in at least five subpopulations, as suggested by the sum of squares curve (Figure S 3.1). The subpopulations were also explored by PCA, with the genotypes colored according to the groups previously determined with STRUCTURE, as described by Evanno, Regnaut, and Goudet (2005) with the admixed group considered as a subpopulation, $K=3$, (Figure 3.1B) and according to the results obtained with the *k*-means clustering method (Hartigan and Wong 1979) ($K=5$, Figure S 3.2). The PCA (Figure 3.1B) revealed a clear subdivision into groups for $K=3$, but the proportions of the variance explained by principal components 1, 2, and 3 were very low, at 3%, 2% and 1%, respectively. For $K=5$ (Figure S 3.2), a clear separation of the groups was observed for dimensions 1 / 2 and 1 / 3. However, when dimensions 2 / 3 or 1 / 4 were used, group 3 was the only group that could be distinguished clearly. The IBD analysis revealed a correlation between genetic distance and physical distance between sampling points (Spearman's $\rho = 0.33$ and p -value = 10^{-04}).

Linkage disequilibrium, genetic diversity and genetic load

SNP density was homogeneous (Figure S 3.3) throughout the genome (mean of 5,500 SNPs per chromosome) and chromosomes (mean of 0.2 SNPs per kb). The extent of LD decay ($r^2 < 0.2$) was calculated per chromosome; it ranged from 307 bp on chromosome 16 (Figure S 3.4A) to 8 kb on chromosome 6 (Figure S 3.4B) with a mean value of 2.2 kb (method from Hill and Weir 1988). SNPs with a predicted *high* impact accounted for 0.75% of SNPs, and these SNPs were the least represented group. Similar proportions of SNPs were predicted to have *moderate* and *low* impacts (ca. 17%; Table S 3.1). SNPs classified as *modifiers* were the most abundant (65%). The distribution of each category of SNPs was similar between chromosomes. The number of SNPs for each estimated effect is detailed in Table S 3.2. There were no significant differences in the accumulation of deleterious alleles between subpopulations 1 and 2 and the admixed group, although accumulation rates were slightly lower in subpopulation 1 than in subpopulation 2 and the admixed subpopulation (Figure S 3.5).

Hardy Weinberg equilibrium was tested for each SNP in each subpopulation. The number of SNPs in HW disequilibrium (p -value < 0.05) was similar for subpopulation 1 and the admixed subpopulation (14,383 and 12,248, respectively, corresponding to 14% and 12% of the analyzed SNPs, respectively). The number of SNPs in HW disequilibrium in subpopulation 2

was 7,428 (7% of the analyzed SNPs), which is lower than that in the other subpopulations. Considering all subpopulations together, the number of SNPs displaying significant HW disequilibrium was 31,905. Considering all the SNPs in each subpopulation, the differences in HW disequilibrium were not significant (p -value = 0.57 for subpopulation 1, 0.70 for subpopulation 2, and 0.60 for the admixed subpopulation). The mean value of Tajima's D calculated for 10 kb windows was 0.59 for subpopulation 1, 0.48 for subpopulation 2, 0.58 for the admixed subpopulation and 0.93 for all subpopulations considered together.

Genome-environment association

The structure of the population followed a geographic pattern (Figure 3.2). The elevation of the sampling sites differed considerably (Figure S 3.6) ranging from 722 to 2,295 m. The mean elevation of each subpopulation made it possible to separate the groups easily (Figure 3.3). Three QTL for elevation were identified on chromosomes 2 (p -value = 9.60×10^{-08}), 7 (p -value = 4.24×10^{-08}), and 15 (p -value = 4.61×10^{-10} ; Figure 3.4). Considerable variation was observed for environmental variables, with GSR ranging from 395 to 581 mm, HYB from 6,932 to 9,326 and DI ranging from -139 to -29 (Figure S 3.7).

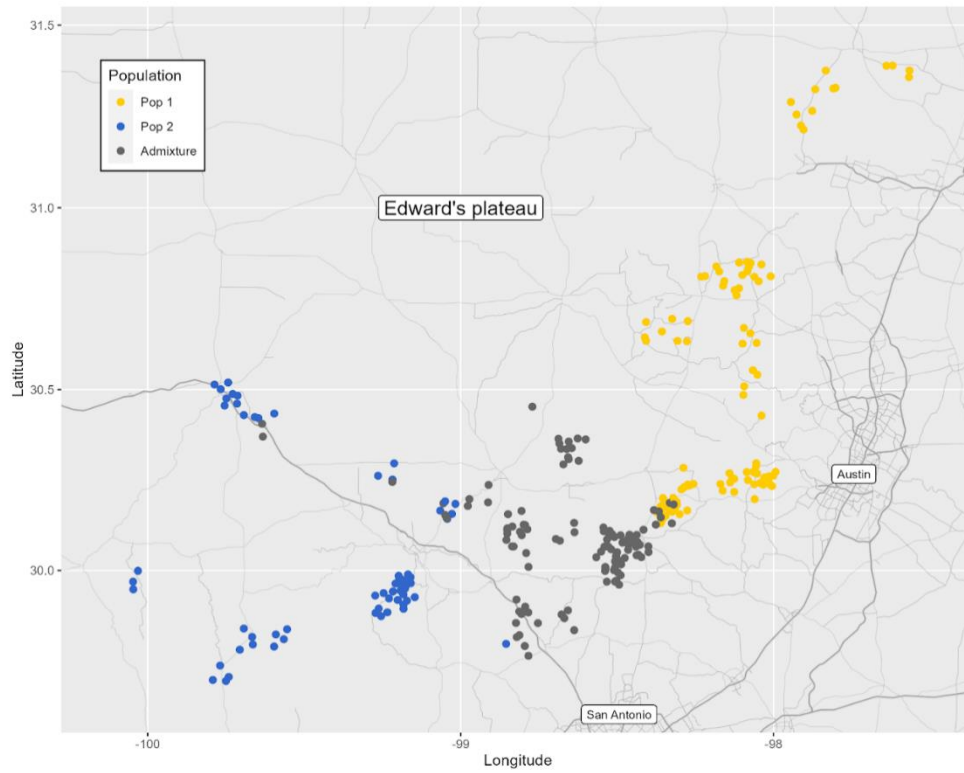


Figure 3.2 : Geographic position of the sites from which plants were sampled in Texas (the genotypes from the same mother plant have been jittered to facilitate observation)

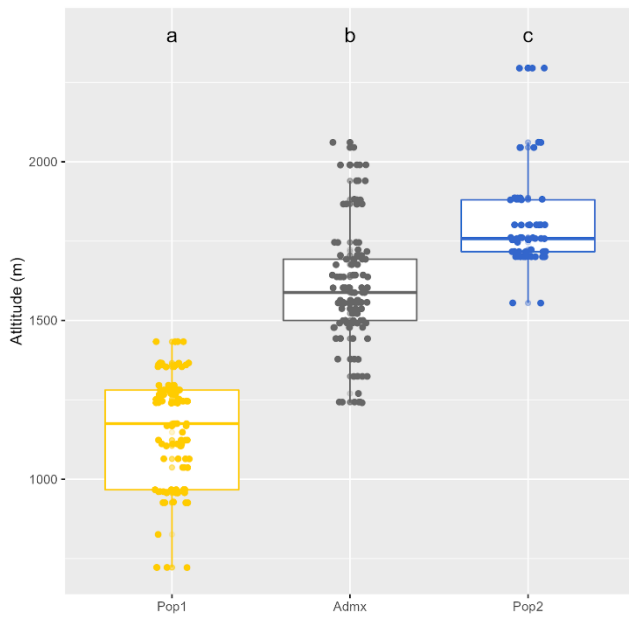


Figure 3.3 : Boxplot of the elevation of the various subpopulations identified by STRUCTURE

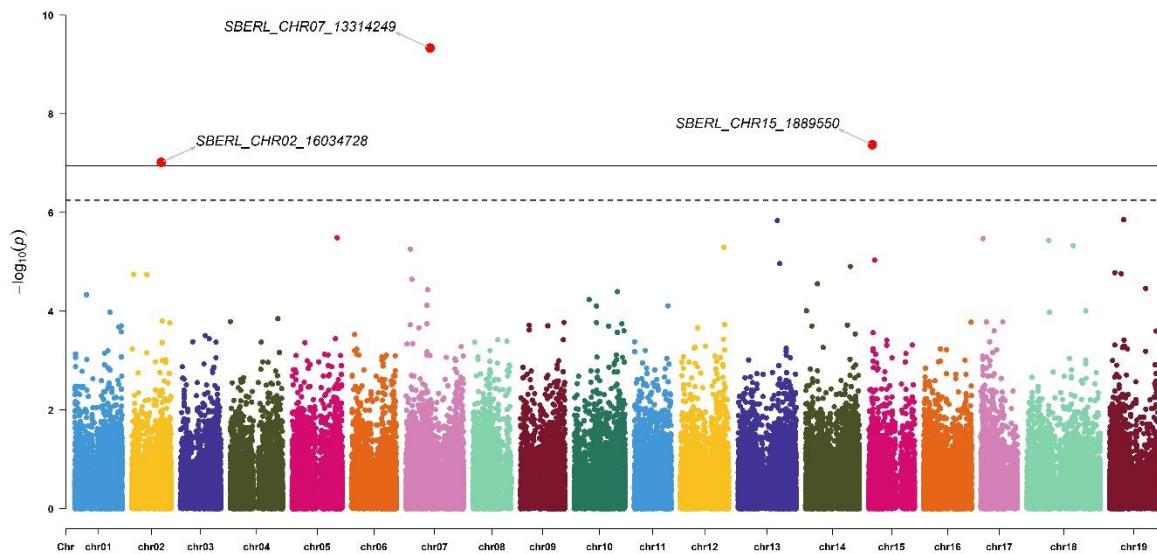


Figure 3.4 : Manhattan plot for SNP associations with elevation. The thresholds were calculated by the Bonferroni method (α/N_{SNP}) for $\alpha = 0.05$ (dotted line) and 0.01 (solid line). Significant signals are highlighted in red, and the corresponding QQ plot is presented Figure S 3.10

Subpopulation 1 was located in an area that was warmer and damper than the areas occupied by the other two subpopulations, with a higher GST49, GSR49, RRSPR, HST, WFR and SFR. The HI value revealed a *very warm climate* (>3000) for all subpopulations and was significantly higher for subpopulation 1 than for the other populations (Figure S 3.7J); the CI value (>18) indicated *warm nighttime* conditions for subpopulation 1.

Subpopulation 2 was located in a region that was drier and cooler than that occupied by subpopulation 1, with a moderate risk of frost during the spring (<12°C; Figure S 3.7H) and temperate nights (14-18°C; Figure S 3.7K). Based on DI, the three subpopulations were considered to come from a *moderately dry* area, with a few genotypes from subpopulation 2 and the admixed subpopulation classified as coming from a *very dry* area, significantly drier than that for subpopulation 2 as a whole (Figure S 3.7L).

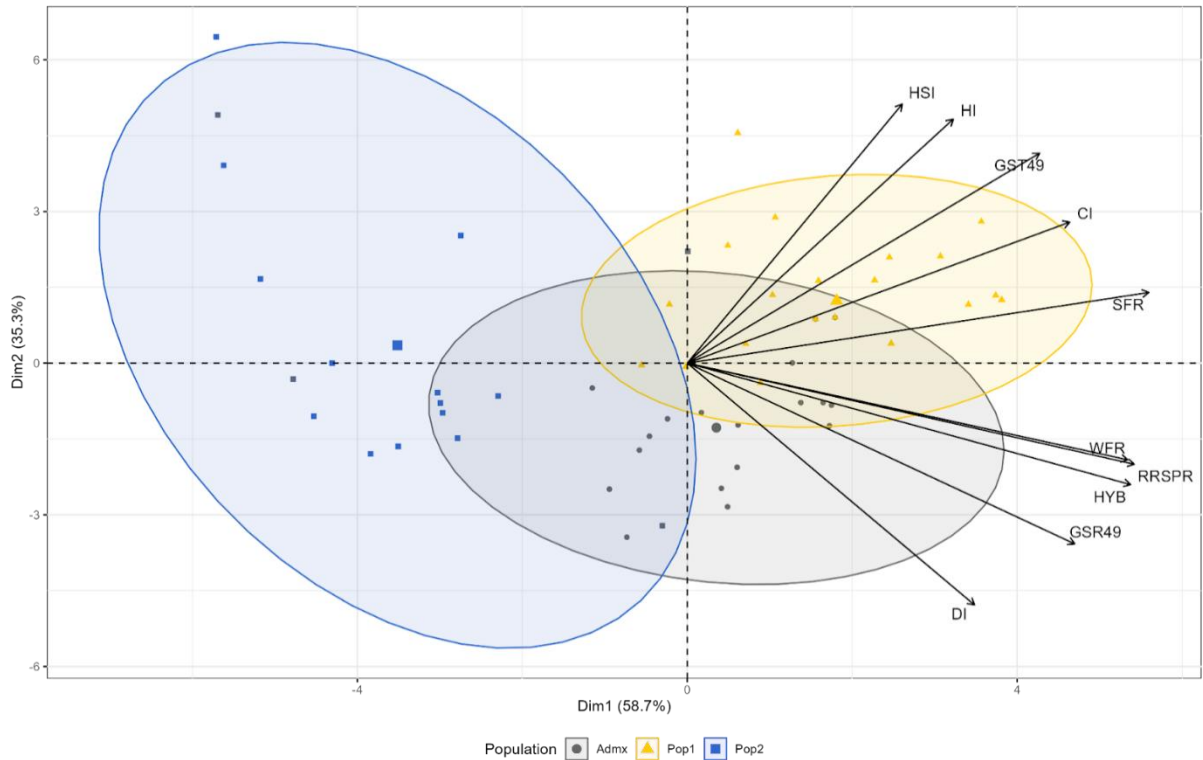


Figure 3.5 : PCA of the environmental parameters accessed via the TerreClimate platform (Abatzoglou et al., 2018). The following variables were extracted : growing season temperature between April and September (GST49, GST, Jones et al., 2006), growing season rainfall between April and September (GSR49, GSR, Bois et al., 2017), sprintime rainfall (RRSPR, from April to July), Branas hydrothermal index (HYB, Branas et al., 1946), winter cold damage index (WFR, Bois et al., 2014), Hugin index (HI, Tonietto and Carbonneau, 2004), cool night index (CI, Tonietto and Carbonneau, 2004), and dryness index (DI, Tonietto and Carbonneau, 2004). Each group identified by STRUCTURE is indicated and ellipses are drawn with 95% confidence level.

As correlations were found between environmental parameters, PCA was performed to capture environmental variability in an integrated manner (Figure 3.5). The first two principal components (PC) explained 94% of the variance. An analysis of the genome-environment association for the PC1 trait identified eight significant QTL on chromosomes 1, 4, 5, 6, 7 (2), and 19 (Figure 3.6). For PC2, seven significant QTL were detected on chromosomes 7 (2), 9 (2), 10, 14 and 18 (Figure 3.7). The significant QTL corresponded to SNPs classified as *modifiers*, or with *low* or *moderate* impact, and the genes concerned had basic molecular functions potentially involved in various biological pathways (Table 3.1).

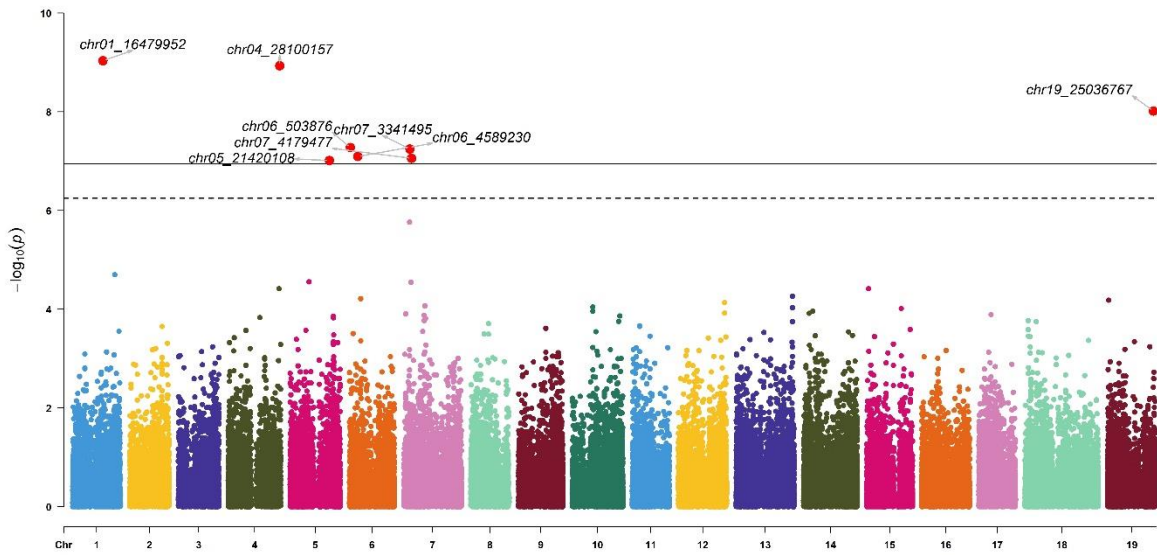


Figure 3.6 : Manhattan plot for the PC_1 trait (principal component from the PCA on environmental parameters). The thresholds were calculated by the Bonferroni method (α/N_{snp}) for $\alpha = 0.05$ (dotted line) and 0.01 (solid line). Significant signals are highlighted in red. The corresponding QQ plot is presented in Figure S 3.11A.

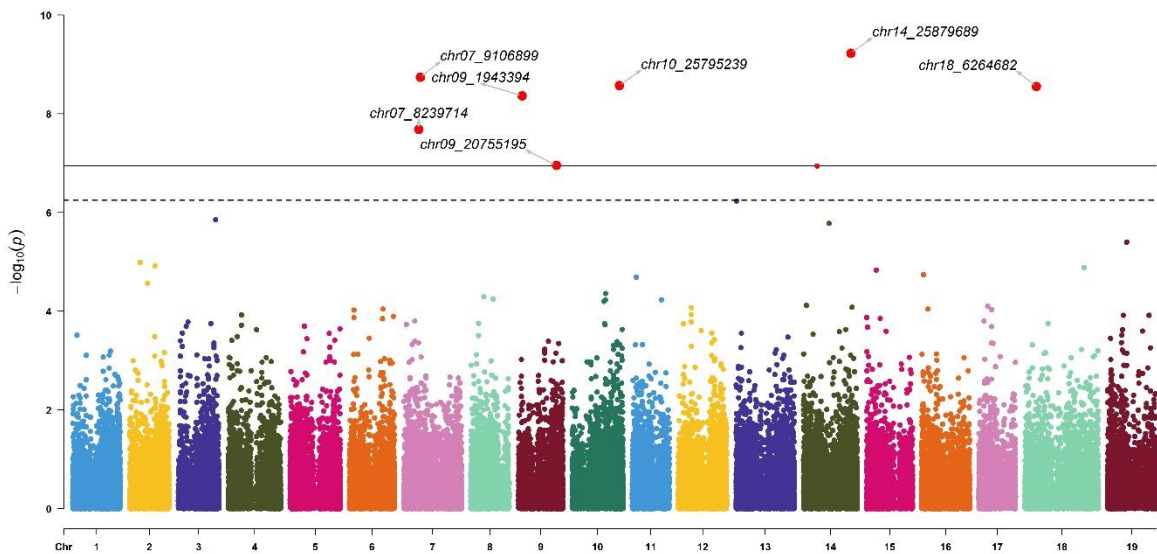


Figure 3.7 : Manhattan plot for the PC_2 trait (principal component from the PCA on environmental parameters). The thresholds were calculated by the Bonferroni method (α/N_{snp}) for $\alpha = 0.05$ (dotted line) and 0.01 (solid line). Significant signals are highlighted in red. The corresponding QQ plot is presented in Figure S 3.11B.

Table 3.1 : Markers associated with environmental parameters

Trait	SNP	Chr	Position	n	FDR Adjusted P-values	maf	Effect	Impact	Gene	Allias	Molecular function
Alt	chr02_16034728	chr02	16034728	281	2,8E-03	0,25	5_prime_UTR_variant	MODIFIER	Vitvi02g00558	VIT_00s0229g00020	Asparagine-tRNA ligase
Alt	chr07_13314249	chr07	13314249	281	4,1E-05	0,07	missense_variant	MODERATE	Vitvi07g02904	VIT_00s0267g00030	Multiple-splicing variant
Alt	chr15_1889550	chr15	1889550	281	1,9E-03	0,33	downstream_gene_variant	MODIFIER	Vitvi15g01070	VIT_15s0046g01920	Ferric reduction oxidase 2
PC1	chr01_16479952	chr01	16479952	277	5,2E-05	0,06	3_prime_UTR_variant	MODIFIER	Vitvi01g00842	VIT_01s0026g00810	Unknown protein
PC1	chr04_28100157	chr04	28100157	277	5,2E-05	0,08	intron_variant	MODIFIER	Vitvi04g01724	VIT_04s0044g01570, VIT_04s0044g01580, VIT_04s0044g01590, VIT_04s0044g01600	Multiple-splicing variant
PC1	chr05_21420108	chr05	21420108	277	1,1E-03	0,08	3_prime_UTR_variant	MODIFIER	Vitvi05g02116	VIT_05s0062g00740	Glycosyltransferase
PC1	chr06_503876	chr06	503876	277	1,0E-03	0,31	missense_variant	MODERATE	Vitvi06g01533	VIT_06s0080g00940	Nitrilase
PC1	chr06_4589230	chr06	4589230	277	1,1E-03	0,47	upstream_gene_variant	MODIFIER	Vitvi06g01246	VIT_06s0009g03560	RNA binding
PC1	chr07_3341495	chr07	3341495	277	1,0E-03	0,09	downstream_gene_variant	MODIFIER	Vitvi07g01826	VIT_07s0031g01490	Metal ion binding
PC1	chr07_4179477	chr07	4179477	277	1,1E-03	0,10	downstream_gene_variant	MODIFIER	Vitvi07g01729	VIT_07s0031g00450	(BHLH domain-containing protein) Protein dimerization activity
PC1	chr19_25036767	chr19	25036767	277	2,9E-04	0,06	intron_variant	MODIFIER	Vitvi19g01666	VIT_19s0085g00020	Chromatin binding
PC2	chr07_8239714	chr07	8239714	277	3,1E-04	0,08	5_prime_UTR_variant	MODIFIER	Vitvi07g01381	VIT_00s0742g00030	Pyrimidine nucleotide-sugar Transmembrane transporter activity
PC2	chr07_9106899	chr07	9106899	277	6,2E-05	0,12	synonymous_variant	LOW	Vitvi07g02508	VIT_07s0255g00010	Nuclear localization sequence binding
PC2	chr09_1943394	chr09	1943394	277	7,7E-05	0,42	upstream_gene_variant	MODIFIER	Vitvi09g01386	VIT_09s0054g00750, VIT_09s0054g00760, VIT_09s0054g00770	Multiple-splicing variant
PC2	chr09_20755195	chr09	20755195	277	1,3E-03	0,07	missense_variant	MODERATE	Vitvi09g01590	VIT_09s0002g03920	PGG domain-containing protein
PC2	chr10_25795239	chr10	25795239	277	6,2E-05	0,19	missense_variant	MODERATE	Vitvi10g00114	VIT_00s2188g00010	Trensmembrane transporter activity
PC2	chr14_25879689	chr14	25879689	277	5,2E-05	0,06	splice_region_variant&intron_variant	LOW	Vitvi14g01620	VIT_14s0219g00080	Glycosyltransferase activity
PC2	chr18_6264682	chr18	6264682	277	6,2E-05	0,09	downstream_gene_variant	MODIFIER	Vitvi18g00553	VIT_18s0001g07900	Transcription factor

3.5 Discussion

De novo whole-genome sequencing of *V. berlandieri* made it possible to explore the genetic structure of a wild *V. berlandieri* population with genome-wide molecular markers. We identified two distinct subgroups that could be explained by isolation by distance. However, no significant differences in genetic diversity or genetic load were found between subpopulations. Using geographic coordinates and climatic data from meteorological stations, we characterized the environments from which the subpopulations were collected and identified several QTL associated with environmental conditions and agronomic indices of climatic conditions.

The complexity of the plant genome renders short-read sequencing highly challenging, due to the large numbers of repetitive sequences and heterozygosity (Schatz, Witkowski, and McCombie 2012). We used long-read sequencing, which overcomes these problems, in this study. The low level of LD in wild *Vitis* species is well known (Myles et al. 2010; 2011; Marrano et al. 2018; Liang et al. 2019; Péros et al. 2021). Our results confirm the rapid LD decay (about 2 kb) reported in previous studies. This rapid LD decay drives the retention of as many SNPs as possible, making it possible to capture a maximum of the genetic variability in the

population (Remington et al. 2001; Myles et al. 2011; Flutre et al. 2019). We obtained a set of 104,378 SNPs, which we used for fine genetic association studies. We ensured that the maximum level of genetic diversity was retained, by including genotypes with up to 60% missing data in our analyses.

Genetic structure

Wild *Vitis* species are characterized by considerable genetic diversity (This, Lacombe, and Thomas 2006). The genetic diversity and the relationships between these species and varieties has already been investigated, as interspecific hybrids and rootstocks showed have been shown to display greater genetic diversity than varieties of *V. vinifera* (Andrés et al. 2007; Laucou et al. 2011). The wild grapevines (*V. vinifera* ssp. *sylvestris*) of the Anatolia region, which is considered to be the center of origin of grapevine (McGovern 2003), are highly diverse (Ergül et al. 2011; Ekhvaia et al. 2014). However, the genetic diversity of wild grapevines in the European region is lower (Di Vecchi-Staraz et al. 2009; Lopes et al. 2009), probably mirroring the human footprint on these populations. The genetic diversity of *Vitis* has been also explored in the Americas, revealing different groups in South America (Martinez et al. 2006) and North America (Péros et al. 2021), and considerable diversity between species. However, genetic diversity and genetic structure within *Vitis* species has been little explored. We addressed this issue here, by studying the population structure and genetic diversity in *V. berlandieri*, a species of considerable interest for the breeding of grapevine rootstocks.

The population structure detected in our study could be explained geographically. The two subpopulations were from physically close locations and were poorly differentiated ($F_{ST} = 0.036$ and 0.060 for subpopulations 1 and 2, respectively, in STRUCTURE analysis), probably due to the small size of the geographic area used for sampling. Moreover, the F_{ST} between the two subpopulations was 0.032 . A low level of differentiation at regional level has also been observed in other perennial species, such as *Fagus sylvatica* (Buiteveld et al. 2007; Pluess et al. 2016), *Prunus sibirica* (Wang et al. 2014) and *Malus sieversii* (Richards et al. 2009). This poor differentiation between subpopulations reveals the minor impact of this genetic structure, reducing the risk of false-positive detection in GWAS models (Santure and Garant 2018). The sampling area in our study was restricted to the region in which *V. berlandieri* is

endemic, but this species extends over a larger area (southern New Mexico, south-western Texas and northern Mexico; Galet 1988) with different soil and climatic conditions. Greater diversity might, therefore, be expected for a larger sampling area. The two non-admixed subpopulations could be characterized as a “northern” and a “southern” subpopulation, with a significantly different mean elevation between these two subpopulations (Figure 3.3).

The five clusters were well distinguished geographically (Figure S 3.8), but elevation divided the total population into three, rather than five subpopulations (Figure S 3.9). We, therefore, considered a genetic structure based on two subpopulations for this geographical area (plus an admixed subpopulation). We found a significant correlation between genetic relatedness and physical distance that was explained by a phenomenon of isolation by distance, consistent with the difference in elevation between the two subpopulations. We took the significant results for IBD into account in the GEA analysis, using kinship information to control for false discovery rate. IBD may also have affected the STRUCTURE results, leading to the detection of false genetic subgroups (Perez et al. 2018). In this study, genetic structure was also controlled by incorporating the proportions of ancestry for each genotype from STRUCTURE.

According to Kimura’s neutral theory of evolution (1968), most new mutations in a population are deleterious or neutral. The number of deleterious alleles may be higher in domesticated plants and animals than in wild species (Wallace, Rodgers-Melnick, and Buckler 2018). Hill-Robertson interference may result in an accumulation of deleterious mutations in genomes, reducing the efficacy of selection (Hill and Robertson 1966). Deleterious variants are hard to predict in plants (Kono et al. 2018). We used snpEff, to predict deleterious variants and to investigate their relationship to genetic structure. We found no difference in the proportion of deleterious alleles between the *V. berlandieri* subpopulations. We were therefore unable to confirm that the admixed subpopulation had a lower genetic load due to greater mixing (Peischl et al. 2013). However, other sequence-based estimates, such as the efficacy of selection (Chen, Glémin, and Lascoux 2017), may shed light on the ways in which natural selection deals with the accumulation of deleterious mutations. The link between domestication and the accumulation of deleterious mutations remains unclear, but this knowledge might be directly useful in breeding programs. Günther and Schmid (2010) classified 20% of polymorphic sites as deleterious variants in rice and *Arabidopsis* and found the genetic load to be lower in wild rice than in domesticated rice, consistent with the

hypothesis of a “cost of domestication” (Lu et al. 2006). However, Kim et al. (2021) reported that the deleterious variant burden was lower in domesticated soybean than in wild soybean. Domestication has different impacts on annual and perennial plants (Gaut, Díez, and Morrell 2015), because perennials are mostly propagated vegetatively, limiting the “cost of domestication”. Nevertheless, vegetative propagation has resulted in the fixation of deleterious mutations in cassava (Ramu et al. 2017) and grapevine (Zhou et al. 2017), both of which are both perennials.

Adaptation to the environment

The sampling area in Texas is known locally as “The Hill Country”, highlighting the alternation between valley and hills. Its vegetation changes with elevation and the various environmental pressures would also be expected to vary with elevation, accounting for the variation of a large set of environmental variables (e.g. temperature, humidity, edaphic conditions). For this reason, despite to the smaller size of the area sampled in this study than in previous studies on grapevine (Aradhya et al. 2003; Péros et al. 2011; 2015; 2021; Bacilieri et al. 2013), we were able to highlight the existence of different climatic regions for the three subpopulations. Subpopulation 1 occurred in a hot and humid area, probably resulting in higher biotic pressure (Bois, Moriondo, and Jones 2014), with more efficient photosynthesis and secondary metabolite synthesis (Tonietto and Carbonneau 2004). Subpopulation 2 was found in an area with a cooler climate and lower rainfall levels during the growing period, resulting in a larger water deficit. Different environmental pressures would be expected to apply in these areas of different climatic conditions, potentially leading to insular subpopulation adaptation. This result is consistent with the previous observations of Rives (1974), who reported strong phenotypic diversity between wild species, such as *V. riparia*, *V. rupestris* and *V. berlandieri*, growing in Texas, USA, in terms of morphology, pathogen tolerance and precocity. In particular, Rives reported that *V. berlandieri* plants from the north had hairy leaves and ribbed shoots, whereas those from the south were almost glabrous, with smooth stems. These observations are consistent with our results revealing high levels of phenotypic and genetic variability in this species.

The detected markers associated with environmental variability may reflect genetic regions relating to local adaptation (Williams 1996) with potential for use as indicators for the

prediction of phenotypic variation for adaptive traits (Lasky et al. 2015). GEA studies have detected associations between genetic factors and specific environmental conditions in nature, revealing markers responsible for driving local adaptation or “ecoclines” (Huxley 1938). This method led to the detection of QTL associated with broad environmental traits in *Arabidopsis* (Frachon et al. 2018), barley (Chang et al. 2022), sorghum (Lasky et al. 2015; Menamo et al. 2021), sunflower (Todesco et al. 2020), bean (Ariani and Gepts 2019; Elias et al. 2021), five alpine Brassicaceae species (Zulliger, Schnyder, and Gugerli 2013), and strawberry (Hu et al. 2022). Moreover, these markers can be genotyped in germplasm collections to improve estimates of the genetic diversity present in the collection and to select the best candidates for breeding programs. In this study, 18 SNPs associated with environmental traits were highlighted. The GEA analysis identified three QTL associated with sampling site elevation. The sequence of chr02_16034728 is related to an asparagine-tRNA ligase (Schimmel 1987). Asparagine is involved in nitrogen transport in plants and asparagine accumulation is induced by multiple stresses, including mineral deficiencies, drought, salt, toxic metals and pathogen attack (Lea et al. 2007). The chr07_13314249 marker is associated with multiple-splicing variants and chr15_1889550 matches with AT1G01580 in the *A. thaliana* genome, which has been shown to be related to ferric reduction oxidase 2 (Kim et al. 2019). Iron is involved in chlorophyll biosynthesis, photosynthesis and nucleotide synthesis (Kim and Guerinot 2007). Elevation would be expected to affect a large set of environmental variations linked to a number of different metabolic pathways. The PCA on environmental parameters extracted from the TerraClimate platform revealed associations with general environmental variability in each subpopulation. Eight QTL were identified for PC1, including chr05_21420108, which is linked to glycosyltransferase activity (Ramasamy et al. 2005) and mostly affects sugar metabolism (Keegstra and Raikhel 2001) and chr06_503876, which is related to nitrilase enzyme synthesis (Piotrowski and Volmer 2006). Nitrilases have been reported to be involved in plant-microbe interactions (Howden and Preston 2009). chr06_4589230 is involved in RNA binding, chr07_3341495 is thought to be involved in metal ion binding and chr19_25036767 is thought to be involved in chromatin binding (Gaudet et al. 2011). Seven QTL involved in diverse metabolic activities have been detected for PC2: pyrimidine nucleotide-sugar transmembrane transporter activity (chr07_8239714, Hadley et al., 2014), nuclear localization sequence binding (chr07_9106899, Gaudet et al. 2011), transmembrane transporter activity (chr10_25795239, Camon et al. 2005) and a transcription

factor (chr18_6264682, Gaudet et al. 2011). Like chr05_21420108 for PC1, chr14_25879689 is associated with glycosyltransferase activity (Camon et al. 2005). Finally, some of the metabolic pathways identified in our GEA study, such as sugar, iron and asparagine metabolism, may be involved in adaptation.

The genotyping of *V. berlandieri* germplasm collections for the molecular markers identified here is of potential interest for the selection of individuals carrying favorable alleles for a particular environmental stressor, to facilitate the selection of genetic resources better adapted to local cultivation environments. Here, we identified 18 QTL as correlated with environment variability; two had high F_{ST} values — 0.189 and 0.221 for chr04_28100157 (detected in GEA for PC1) and chr07_9106899 (detected in GEA for PC2), respectively — corresponding to strong genetic differentiation between subpopulations at these loci (Wright 1984; Weir and Cockerham 1984). However, these results require confirmation by further studies based on genetic engineering or the testing of these genotypes in a common garden.

3.6 Conclusion

Our results confirm the existence of considerable genetic diversity in the *V. berlandieri* genetic background, even over a relatively small sampling area (about 40,000 km²). The analysis of genome-environment association revealed genetic markers associated with the climatic conditions in the sampling areas. These associations should highlight genetic regions involved in the adaptation of plants to different environmental conditions. Wild genotypes constitute valuable resources that could be subjected to more precise selection and included in breeding programs. However, before their inclusion in breeding programs, these genotypes will need to undergo assessments of their agronomic performance.

3.7 Acknowledgments

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3.9 Supplemental data

Table S 3.1 : Impact of SNPs predicted by the snpEff® program as a function of position in the genome : i) high if they cause a loss of protein function, ii) moderate if they alter protein effectiveness, iii) low if they have no impact on the protein and iv) modifier for non-coding variants. The number of SNPs for each impact category is indicated par chromosome.

Impact	chr01	chr02	chr03	chr04	chr05	chr06	chr07	chr08	chr09	chr10	chr11	chr12	chr13	chr14	chr15	chr16	chr17	chr18	chr19	Total
HIGH	30	25	30	36	67	32	62	20	39	45	34	42	59	70	40	47	24	47	38	787
LOW	903	684	815	957	1169	841	1233	747	710	836	699	959	1204	1247	678	874	736	1174	922	17388
MODERATE	853	683	857	841	1543	785	1203	728	685	937	679	913	1393	1406	806	954	653	1244	1052	18215
MODIFIER	3630	3029	2987	3347	4085	2900	4669	2967	3545	3835	2855	3961	4634	4416	2954	2885	2692	5011	3586	67988
Total	5416	4421	4689	5181	6864	4558	7167	4462	4979	5653	4267	5875	7290	7139	4478	4760	4105	7476	5598	104378

Table S 3.2 : Effect of SNPs predicted by snpEff® software according to position in the genome. The number of SNPs belonging to each effect category is indicated per chromosome

Effect	chr01	chr02	chr03	chr04	chr05	chr06	chr07	chr08	chr09	chr10	chr11	chr12	chr13	chr14	chr15	chr16	chr17	chr18	chr19	Total
3_prime_UTR_variant	178	108	190	228	232	161	213	159	194	167	162	166	249	241	163	84	178	205	165	3443
5_prime_UTR_premature_start_codon_gain_variant																				
nt	15	14	9	24	17	18	26	21	12	17	7	16	16	21	11	7	17	30	16	314
5_prime_UTR_variant	112	79	64	100	81	88	126	117	80	78	52	114	115	110	60	68	94	155	82	1775
downstream_gene_variant	822	681	660	838	1134	642	1096	615	737	809	643	758	897	900	627	603	589	1106	871	15028
initiator_codon_variant				1	1						1							1		4
intergenic_region	526	567	433	340	469	407	544	237	740	693	392	847	848	694	561	579	293	809	643	10622
intraonic_variant							24													24
intron_variant	818	602	570	804	842	663	1031	611	687	701	753	797	990	864	574	564	650	849	652	14022
missense_variant	850	674	853	833	1530	780	1202	725	680	932	677	909	1384	1396	802	944	649	1238	1044	18102
missense_variant&splice_region_variant	3	9	4	8	13	5	1	3	5	5	2	4	9	10	4	10	4	6	8	113
non_coding_transcript_exon_variant	6	9					7		1	15	9	3	15		3		2	2		72
splice_acceptor_variant&intron_variant	3	1	3	8	10		2	1	4	1		5	4	2	4		1	5		54
splice_donor_variant&intron_variant	3	1	4	5	3	1	1	1	7	4	3	2	3	1	2	2	2	2	3	47
splice_region_variant	1	3	2	2	2	3	9	3	3	3	1	5	1	2	1		1	3	1	44
splice_region_variant&intron_variant	48	31	49	47	48	54	73	44	37	39	35	50	58	64	32	40	38	52	45	884
splice_region_variant&non_coding_transcript_exon_variant					1						1	1			2				1	6
splice_region_variant&stop_retained_variant	1	3	2			2			1		1			1				1		12
splice_region_variant&synonymous_variant	5	6	3	6	10	8	8	1	4	4	4	5	9	3	3	6	8	12	9	114
start_lost	1			2		1	4	1	2			1		1	2	2				17
start_lost&splice_region_variant											1						1			2
stop_gained	19	16	18	11	30	18	39	12	14	25	17	16	34	46	20	26	15	24	27	427
stop_gained&splice_region_variant	1			1			1				1			1	1					6
stop_lost	6	5	7	9	21	10	15	5	12	15	12	17	17	19	14	15	5	16	8	228
stop_lost&splice_region_variant			1	1	1							1	1			1				6
stop_retained_variant	2	2	1		8	4	4	3	4	2	3	5	1	10	5	4	3	8	4	73
synonymous_variant	832	627	748	877	1082	752	1113	675	649	771	646	877	1119	1146	624	817	669	1067	846	15937
upstream_gene_variant	1168	983	1070	1037	1327	939	1652	1204	1106	1372	844	1276	1520	1607	966	987	886	1885	1173	23002
Total	5416	4421	4689	5181	6864	4558	7167	4462	4979	5653	4267	5875	7290	7139	4478	4760	4105	7476	5598	104378

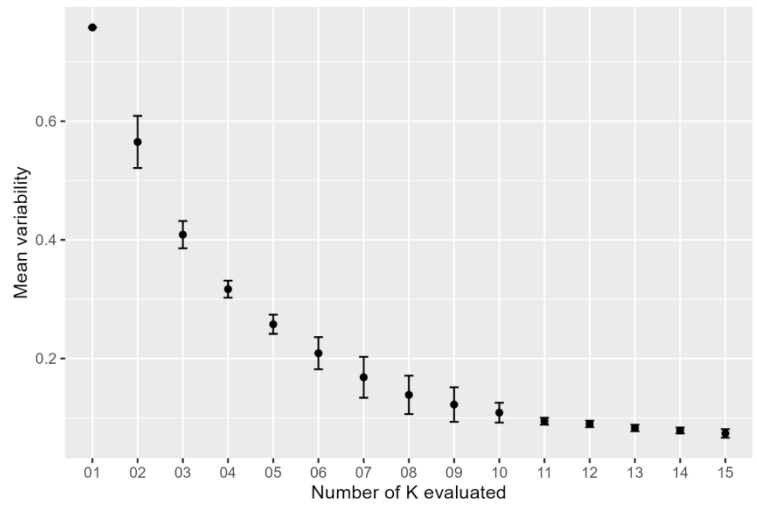


Figure S 3.1 : Mean variability of the within-cluster sum of squares according to the number of populations. The results were obtained by *k*-means clustering with the Hartigan and Wong (1979) algorithm.

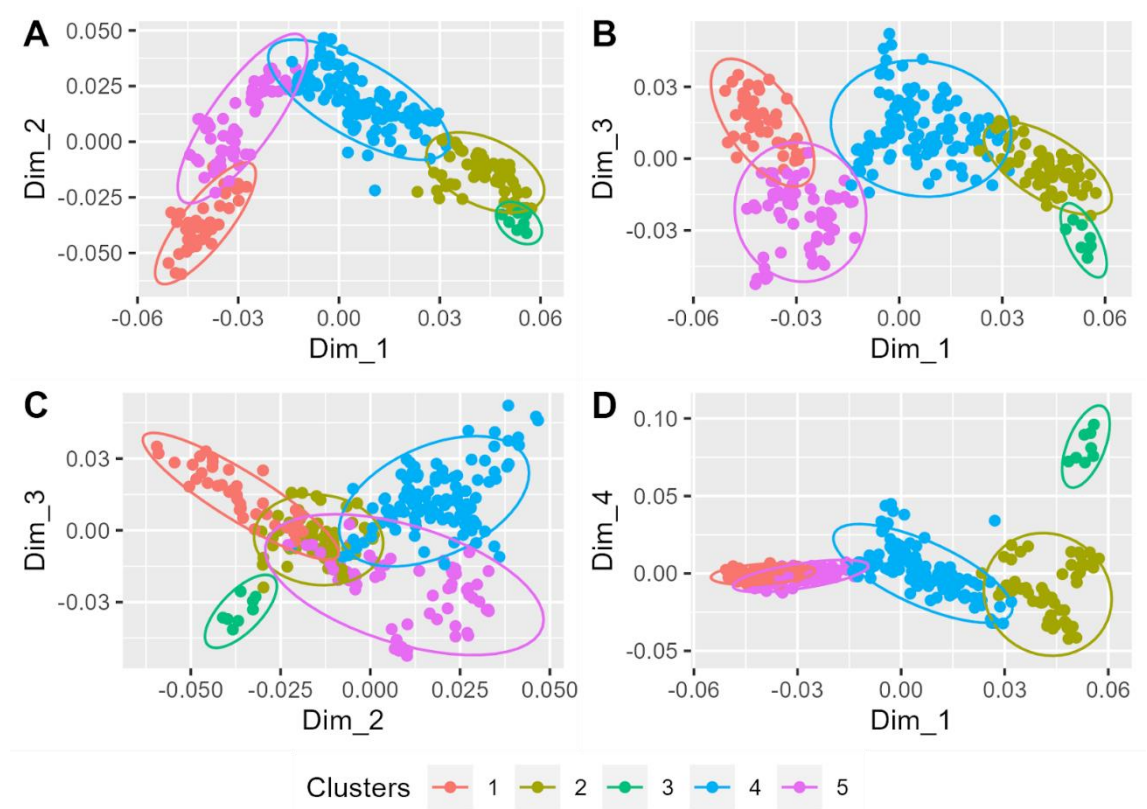


Figure S 3.2 : PCA of each genotype obtained with the 104378 SNPs. Groups are identified according to *k*-means clustering for *K*=5.

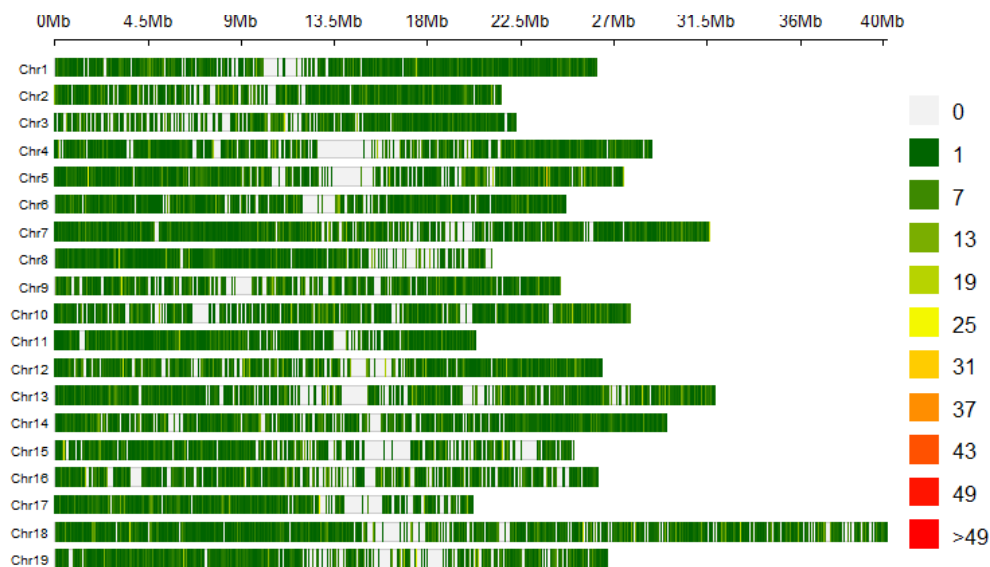


Figure S 3.3 : SNP density per kb obtained by GBS for each chromosome of the *V. berlandieri* genome.

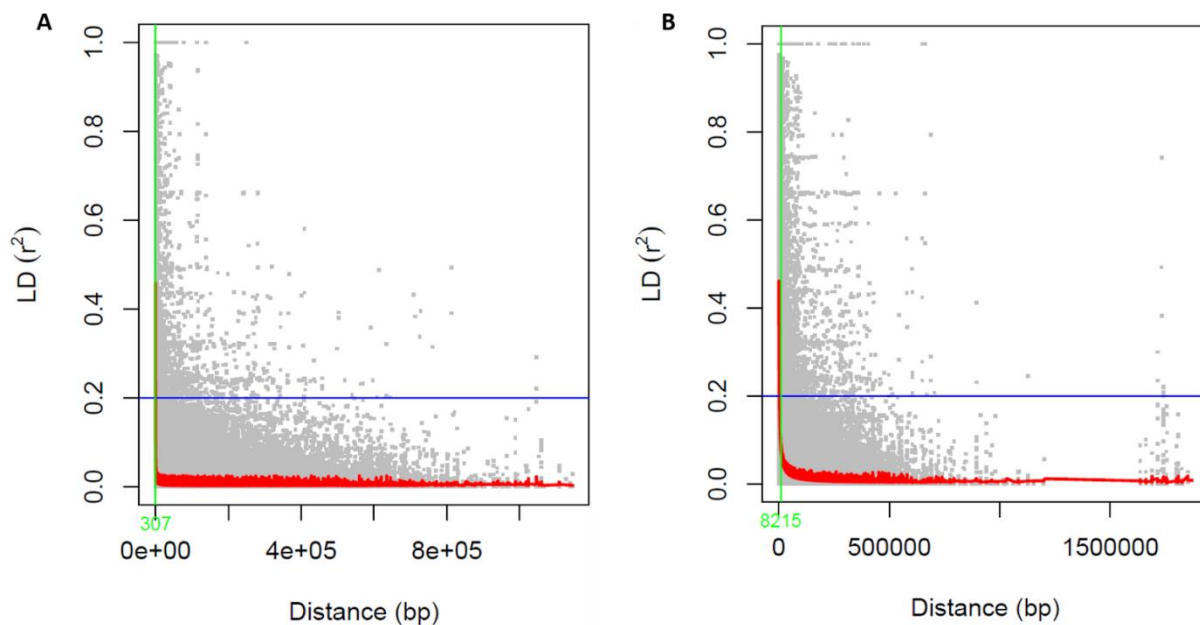


Figure S 3.4 : Linkage disequilibrium on chromosomes 16 (A) and 6 (B). Linkage disequilibrium is calculated for $r^2 < 0.2$ as described by Hill and Weir (1988)

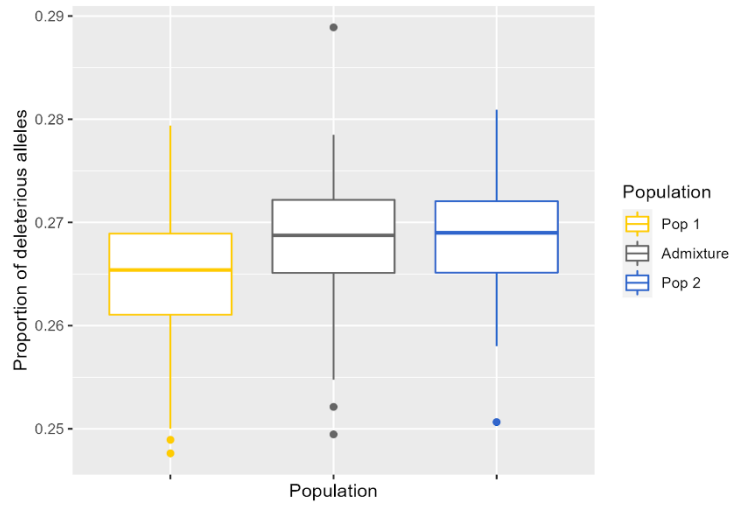


Figure S 3.5 : Proportion of deleterious alleles in the subpopulations. Subpopulations were identified in the STRUCTURE analysis. The proportion of deleterious alleles was calculated as the ratio of alleles for high-impact SNPs over the total number of alleles. The impact of each SNP was predicted by *snpEff*[®] according to the position in the genome and an annotated reference sequence.

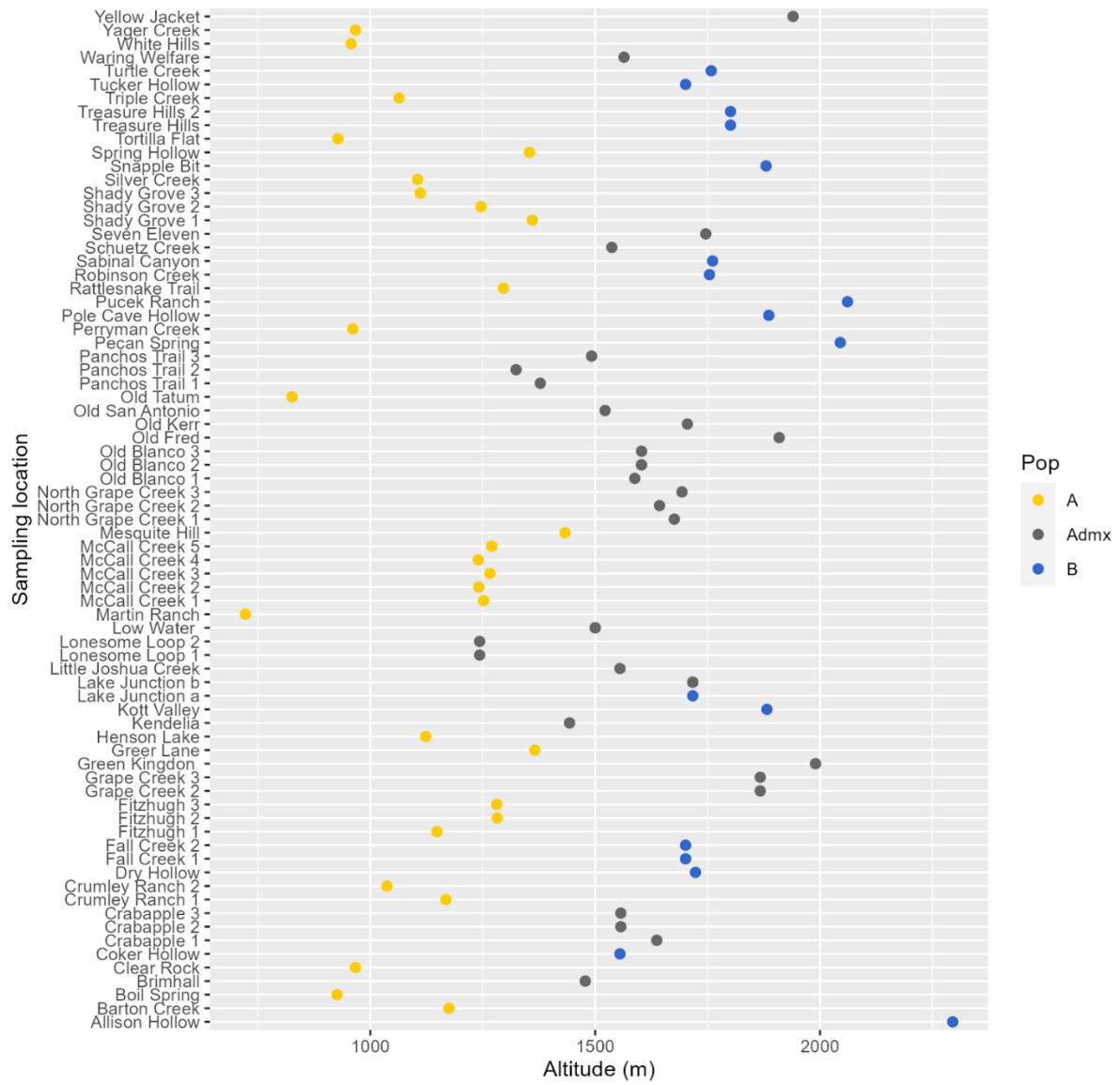


Figure S 3.6 : Elevation of the sampling sites (one sampling site per mother plant). Colores indicate the subpopulations identified by sSTRUCTURE (K=2).

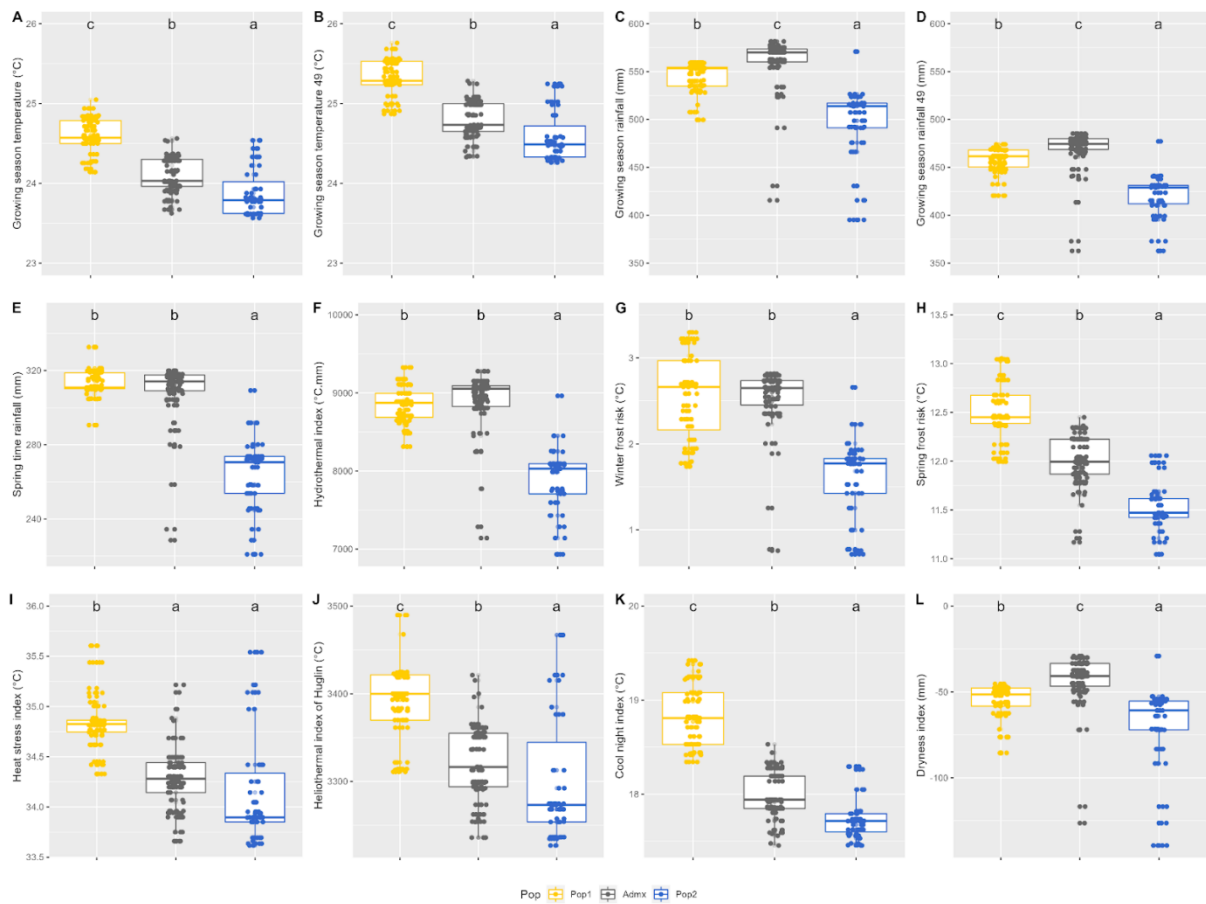


Figure S 3.7 Boxplot of environmental parameters extracted from the TerraClimate platform, including growing season temperature (A), growing season temperature from April to September (B), growing season rainfall (C), growing season rainfall from April to September (D), springtime rainfall (E), hydrothermal index (F), cool night index (K) and dryness index (L) for each subpopulation identified by STRUCTURE. The letters indicate the results of a Tukey test (different letters indicate significant differences).

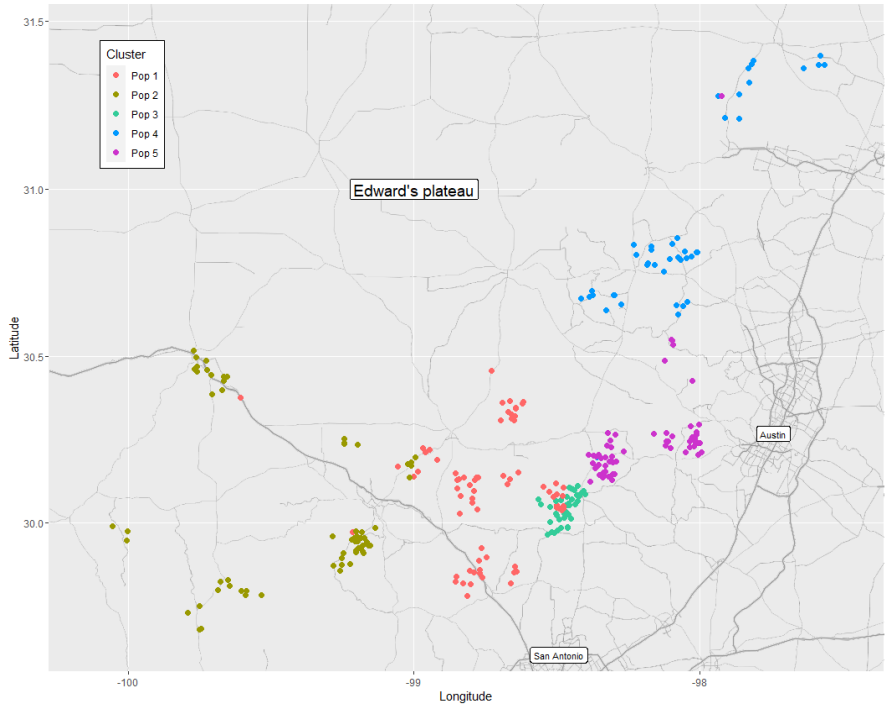


Figure S 3.8 : Position of genotypes according to the origin of the mother plant sampled in Texas each dot corresponds to a genotype from each group identified by the k-means clustering method). If the same mother plant gave rise to offspring of several genotypes, the jitter option was used to make it easier to distinguish between genotypes on the map).

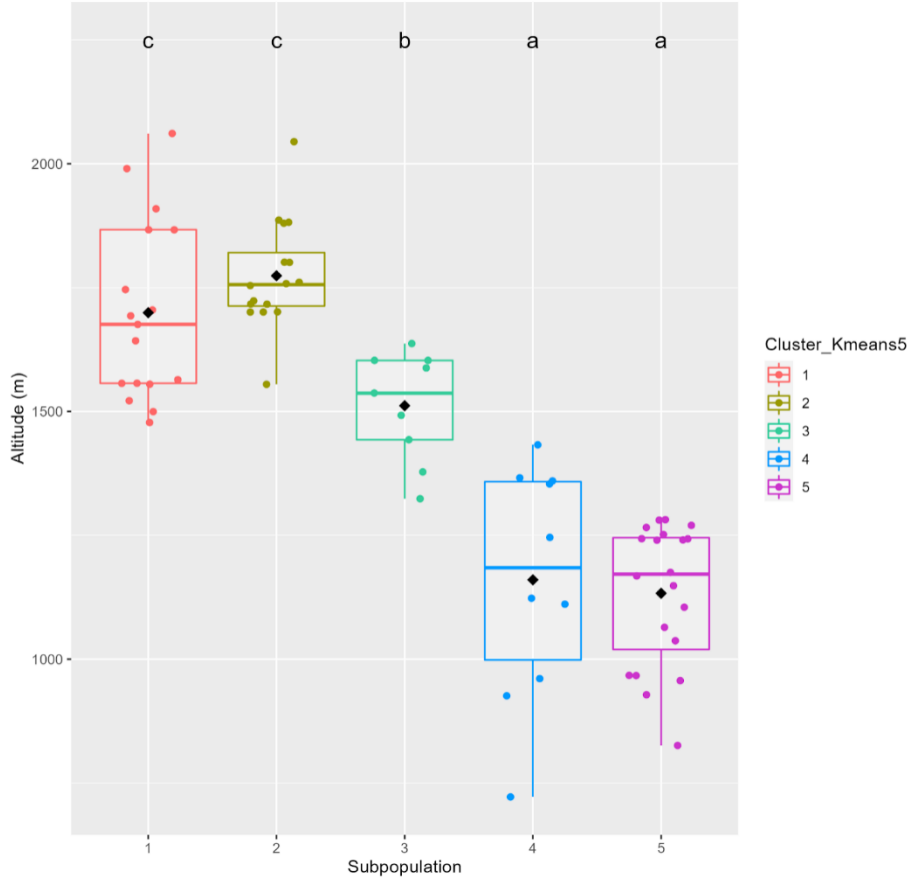


Figure S 3.9 : Mean elevation of the subpopulations identified by the k-means method (K=5).

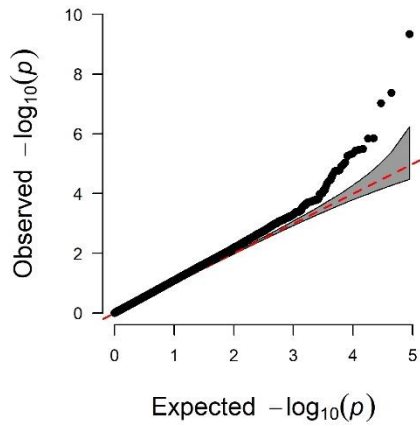
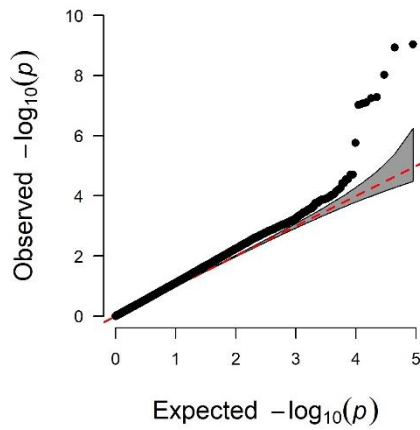


Figure S 3.10 : QQ plot, indicating the distribution of theoretical and observed p-values in the GEA analysis for 'elevation'.

A



B

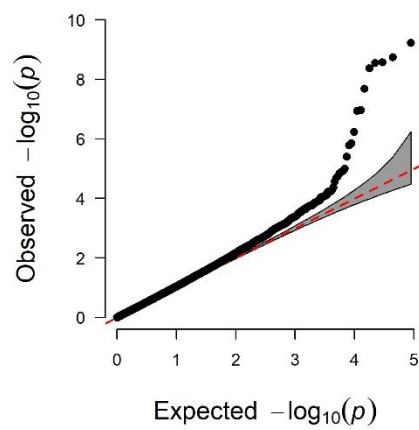


Figure S 3.11 : QQ plot, indicating the distribution of theoretical and observed p-values in the GEA analysis for PC1 (A) and PC2 (B)

Conclusion

In this paper, SNP markers have been used to explore the genetic structure of the wild *V. berlandieri* population, revealing two distinct subpopulations in a restricted geographic area. These results represent the first insight on a specific genetic background diversity on American *Vitis* species. It shows the potential genetic resources available in natural conditions which could be included in grapevine rootstocks breeding programs.

Two climatic regions have been observed for the two subpopulations linked to the altitude of sampling. Then association between the genetic and environment variability have been detected. QTL have been highlighted as being impacted by environment. These genetic hotspots could be associated with the plant adaptation capacity, representing valuable information for breeding.

The de novo long reads whole genome sequencing allowed us to present the first high quality genome reference sequence of *V. berlandieri*. Thanks to genotyping by sequencing (GBS) method, we have been able to extract a set of SNP evenly distributed along the *V. berlandieri* genome.

The genetic structure of the population will be used in next genetic association studies in order to control false positive and negative signals detection (Pritchard et al. 2000).

Chapter 4: Dissecting the genetic architecture of root-related traits in a grafted wild *Vitis berlandieri* population for grapevine rootstock breeding

“Not all those who wander are lost”

J. R. R. Tolkien

Introduction

No study has been done on a grapevine rootstock wild single species population nor at the phenotypic or the genetic level. *V. berlandieri* is the parent of most used rootstocks hybrids in vineyards. It is known to confer tolerance to phylloxera, water deficit, and limestone. Because this species is used as a rootstock, the main phenotypic expression of the genotype has to be measured at the root system level. Moreover, it is well known that *V. berlandieri* genotypes present defaults to root. The identification of the loci involved in the genetic determinism of rooting could be outstanding to discard this usual disadvantage of this genetic background and to keep their agronomical advantages with drought and limestone tolerances. The aim of this chapter, submitted to *Theoretical and Applied Genetics*, 1) is to measure the phenotypic variability that exists in the population of *V. berlandieri*; 2) to carry out a GWAS on the measured traits in order to highlight genetic regions associated with the root-related traits variability; and 3) to compare root system profiles observed in the population with commercial rootstocks genotypes ones, known for their performances in field, in order to detect potentially interesting genotypes for grapevine rootstocks breeding.

Genome-wide association for root-related traits in a grafted wild *Vitis berlandieri* population for rootstock breeding

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4.1 Abstract

In woody perennial plants, quantitative genetics and association studies remain scarce for root-related traits, due to the time required to obtain mature plants and the complexity of phenotyping. In grapevine, a grafted cultivated plant, most of the rootstocks used are hybrids between American *Vitis* species (*V. rupestris*, *V. riparia*, and *V. berlandieri*). In this study, we used a natural population of an American *Vitis* species (*V. berlandieri*) to analyze the genetic architecture of the root-related traits of rootstocks in a grafted context. We studied a population consisting of 211 genotypes, with one to five replicates each ($n = 846$ individuals), plus four commercial rootstocks as control genotypes (110R, 5BB, Börner, and SO4). After two consecutive years of experimentation, the best linear unbiased estimates method revealed root-related traits with a moderate-to-high heritability (0.36 to 0.82) and coefficient of genetic variation (0.15 to 0.45). A genome-wide association study was performed with the BLINK model, leading to the detection of 11 QTL associated with four root-related traits (one QTL was associated with the total number of roots, four were associated with the number of small roots (< 1 mm in diameter), two were associated with the number of medium-sized roots (1 mm < diameter < 2 mm), and four were associated with mean diameter) accounting for up to 25.1% of the variance. Three genotypes were found to have better root-related trait performances than the commercial rootstocks and therefore constitute possible new candidates for use in grapevine rootstock breeding programs.

Keywords: grapevine, GWAS, QTL, root system, heritability, diversity

4.2 Introduction

Climate change is driving a need to adapt to new environmental conditions through many approaches, including the modification of plant material. The roots of the plant manage its nutrient and water absorption. This organ therefore plays a major role in plant physiology and productivity and constitutes a very good target in breeding for plant adaptation (Voss-Fels, Snowdon, and Hickey 2018). The root system has been identified as a target for breeding for abiotic stress tolerance and yield in cereals (Meister et al. 2014; Maqbool et al. 2022). However, the growing conditions in annual crops must also be taken into account when breeding root traits, to optimize root architecture and root system carbon allocation (Lynch 2018).

High levels of phenotypic variability have been observed for root-related traits in *Arabidopsis* (Pacheco-Villalobos and Hardtke 2012) and in annual crops, but few field trials have been performed due to the complexity of root phenotyping in field conditions (Deja-Muyille et al. 2020; Maqbool et al. 2022). There have also been few studies in perennial plants with potentially high levels of root phenotypic variability, such as *Picea* species (Nielsen 1992), poplar (Wullschleger et al. 2005; Krabel et al. 2015; Sun et al. 2019), and other angiosperms (Seago and Fernando 2013). Accordingly, the genetic basis of root-related traits has been explored in several annual species, such as maize (Hochholdinger and Tuberosa 2009; Pace et al. 2015; Zaidi et al. 2016; Bray and Topp 2018; Sanchez et al. 2018) and rice (Courtois et al. 2009; Mai et al. 2014; Biscarini et al. 2016; Phung et al. 2016; Zhao et al. 2018), but much less is known about perennial species, such as ryegrass (Sun et al. 2019) and woody species (Nielsen 1992; Wullschleger et al. 2005; Krabel et al. 2015; Sun et al. 2019).

Grapevine is a major horticultural crop around the world. Since the decimation of grapevine crops due to the phylloxera crisis in Europe, grapevine has been cultivated as a grafted crop. Most of the rootstocks used are hybrids between the American *Vitis* species *V. rupestris*, *V. berlandieri*, and *V. riparia* (Galet 1988). The grafted nature of modern grapevine crops renders the rootstock a major target for root system breeding. Thanks to the interactions that occur between the scion and the rootstock in grapevine, the rootstock is a precious tool for grapevine adaptation (Ollat et al. 2016). The use of *Vitis berlandieri* as a rootstock has been shown to confer a high tolerance to limestone, drought and phylloxera on the scion (Boubals

1966; Galet 1988). However, the rooting and grafting performances of *V. berlandieri* are generally limiting for its direct use as a rootstock, and it is usually crossed with other American species to obtain hybrids, which are widely used in vineyards: 1103P, 110R, Fercal, SO4, and Gravesac (FranceAgrimer, 2018).

Most studies aiming to decipher the genetic architecture of relevant traits for rootstocks have been based on controlled crosses and QTL analysis (Xu et al. 2008; Zhang et al. 2009; Clark et al. 2018; Henderson et al. 2018; Smith, Clarke, et al. 2018; Smith, Smith, et al. 2018). Moreover, only a few of these studies used grafted grapevines (Marguerit et al. 2012; Bert et al. 2013; Tandonnet et al. 2018). Most genome-wide association studies (GWAS) in grapevine have been restricted to *Vitis vinifera* (Fournier-Level et al. 2009; Emanuelli et al. 2010; Myles et al. 2011; Migicovsky et al. 2017; Marrano et al. 2018; Flutre et al. 2019; 2020) or *Vitis spp.* (Yang et al. 2017; Zhang et al. 2017; Laucou et al. 2018; Guo et al. 2019; Liang et al. 2019; LaPlante et al. 2021; Trenti et al. 2021; Wang et al. 2021) germplasm collections. GWAS have never been performed for natural *Vitis* populations or grafted grapevines. Moreover, previous studies have targeted berry traits, water deficit tolerance and cold tolerance, but not the root system.

Broad genetic diversity has been observed in American *Vitis* species (Péros et al. 2021), but the various genetic backgrounds have yet to be explored. In association studies, the high level of genetic diversity in natural populations and the large numbers of recombination events occurring over many generations can be used to narrow down the positions of loci tightly linked to the trait of interest. The use of such studies to investigate root-related traits can, therefore, improve our understanding of the genetic basis of these traits in a perennial species and identify new beneficial alleles for improving grapevine rootstock breeding programs. However, the large number of individuals required to detect significant associations constitutes a real challenge for root-related traits in grapevine, due to the difficulty phenotyping this underground plant organ in a perennial species.

The aims of this study were: i) to characterize root-related traits in a wild American *Vitis* species used for grafting, ii) to perform GWAS for root-related traits in a wild grapevine genetic background (*V. berlandieri*) and iii) to compare the root-related trait performances of wild genotypes with those of commercial rootstocks. Our results reveal the diversity for root-

related traits present in the wild *V. berlandieri* population. In addition, GWAS highlighted promising markers associated with root-related traits in a natural population.

4.3 Materials and Method

Plant material

The plant material used in this study consisted of 286 genotypes originating from 78 mother plants of wild *V. berlandieri* collected from the Edwards Plateau in Texas, USA (see Blois et al. submitted for further details). All the plants were used as rootstocks, onto which we grafted *Vitis vinifera* Riesling (clone 24-209 for two consecutive years, 2019 and 2020). Not all the genotypes were represented every year in the final population, the genotypes present in a given year depending on the success of grafting (Table S1). The commercial rootstocks 110R (*V. berlandieri* cv. Boutin B x *V. rupestris* cv. Martin), SO4 (*V. berlandieri* Rösséguier 2 x *V. riparia* Gloire de Montpellier), Börner (*V. riparia* 183 G x *V. cinerea* Arnold) and 5BB (*V. berlandieri* Rösséguier 2 x *V. riparia* Gloire de Montpellier) (2020 only) were added to the population as control genotypes. The aim was for each genotype to be represented in at least five replicates, where possible. We obtained 181 genotypes (510 individuals) in 2019, and 144 genotypes (336 individuals) in 2020. In total, 211 genotypes were represented, as 846 individuals and 35 commercial rootstocks. Phenotyping was performed the year after grafting. The 2020 plant pool therefore resulted from the grafting performed in 2019 and the 2021 plant pool corresponding to the grafting performed in 2020.

Grafting was performed at the Institute of Grapevine Breeding in Geisenheim, Germany. Shoots were sampled in the field and cut into 20 cm-long pieces in February. All cuttings were stored in wet bags in a cold room (3°C) after Beltanol treatment to prevent fungal contamination. Grafting was performed by a classical mechanical procedure, with an omega graft, in March 2019 and 2020. The grafted material was placed in a warm room for one month, after which, callus quality was evaluated for removal of plants with a low graft quality. The plants were then grown in plastic containers for one month, after which, all plants with good root and vegetative shoot growth were individually potted in a mixture of potting soil and sand and grown in the absence of limiting conditions until November.

Root phenotyping

Plants were pruned after 2 nodes, potted out, washed with pressurized water and stored in a cold room (3°C) at the end of November. The following year (May 2020 and January 2021 for plants grafted in 2019 and 2020, respectively), roots were cut 4 cm below the collar. Scions and rootstocks were measured with a semi-automatic caliper to determine their diameter and weighed. Primary roots were counted and all diameters were measured with the semi-automatic caliper. Roots were sorted according to their diameter. Those with a diameter of less than 1 mm were considered to be *small* roots, those with a diameter of 1 to 2 mm were considered to be *medium-sized* and those with a diameter of more than 2 mm were considered to be *large* roots. The entire root system was dried in a drying oven at 80°C for three days and weighed. The traits measured were root dry weight (RDW), the total number of roots (Tot_Root_NB), total root diameter (Tot_diam), calculated as the sum of all primary root diameters for a single plant, average diameter (Av_Diam), calculated as the mean diameter of all primary roots from the same plant, the number of small roots (NB_Small, diameter < 1 mm), the number of medium-sized roots (NB_Medium, 1 mm > diameter < 2 mm), the number of large roots (NB_Large, diameter > 2 mm), the proportion of small roots (Prop_Small), the proportion of medium-sized roots (Prop_Medium, I), the proportion of large roots (Prop_Large), scion diameter (SD), rootstock diameter on the thinner and wider sides (RSD_1 and RSD_2, respectively) and the weight of the woody part (PW).

Genotyping-by-sequencing (GBS) data and SNP selection

The GBS data were obtained by sequencing accession PRJNA886619 (Blois et al. (submitted)). Only genotypes for which phenotypic data were available were used for SNP filtering ($n=211$). We used the protocol described by Blois et al. (submitted) for SNP calling. VCFtools (Danecek et al., 2011) was used for filtering on minimum depth of 3, maximum missing data of 0.9, minor allele frequency of 0.05 and a minimum mean depth of 20. In total, 102,296 SNPs were retained and 206 genotypes with less than 70% missing data were analyzed.

Statistical analysis

Statistical analysis was performed without the commercial rootstocks. The density curve was calculated with the `stat_lab` function of the `ggdist` package of R with an adjustment of 0.01. The correlations between traits were explored with Pearson's correlation test. Principal

component analysis (PCA) was performed with RDW, Tot_Diam, AV_Diam, Tot_Root_NB, NB_Small, NB_Medium, and NB_Large. The scion and rootstock diameters and plant weight were not considered in this analysis because these traits are not root-related. The proportion of roots in each size class was correlated with the number of roots in each size class. These traits were therefore excluded from the PCA to ensure that the results obtained were not unbalanced. The control commercial rootstocks were considered as additional individuals but were not included in the calculation of coordinates. Missing data were imputed as the mean value for the trait. Only the 30 genotypes with the highest coordinate on each axis were labeled.

Best linear unbiased predictors (BLUPs) were estimated for each trait, to obtain phenotypic values corrected for environmental variability from the genotype replicates and both years of the experiment. The model used was selected according to BIC (best indicator criterion) information

$$P_{ghi} = \mu + G_g + Y_h + W_i + \varepsilon_{ghi} \quad (1)$$

where P_{ghi} is the phenotypic value for genotype (G_g), year of measurement (Y_h) and the weight of the plant (W_i) after shoot and root pruning. ε_{ghi} is the residual variance. Plant weight was used to correct phenotypic data because it had affects the carbon reserves of the plant and therefore has an impact on root growth. Genotype was considered as a random effect in the model, to obtain a variance-covariance matrix for the calculation of broad-sense heritability (H^2). All the others factors were considered as fixed effects in the model.

The broad-sense heritability of traits was calculated according to equation 2,

$$H^2 = \frac{\sigma_g^2}{\sigma_g^2 + (\sigma_e^2/nrep)} \quad (2)$$

where H^2 is the broad-sense heritability of the trait, σ_g^2 is the variance explained by the genotype effect and $\sigma_e^2/nrep$ is the residual variance extracted from the model divided by the mean number of replicates per genotype in the population.

These models were calculated in R, with the lmer package.

GWAS

We assessed the estimated genetic value of genotypes for each trait whilst avoiding the variance shrinkage associated with predictive models, by calculating the best linear unbiased estimate (BLUE) with a model similar to equation 1 but with all the factors treated as fixed effects in a generalized linear model. The intercept of each genotype was then used as a new phenotypic value in the GWAS. With this procedure, we used only one phenotypic value per genotype for the two years of experiment.

For GWAS, the BLINK model was used in GAPIT3 (Wang and Zhang 2021) with default settings, implementation by major allele and MAF > 0.05 filtration. We retained 87,589 SNPs for further analysis. Population structure was considered as a covariate with $K=2$ (Blois et al. submitted). Kinship was derived from pseudo-QTN information, directly from BLINK. Bonferroni correction was applied to the significance thresholds, which were set at $0.05/n$ and $0.01/n$, where “n” is the number of markers used. The variance explained by significant SNPs were estimated from BLINK results in GAPIT with a mixed linear model.

The genes linked to significant markers were obtained by comparison with the annotated *V. berlandieri* genome, with a window corresponding to the extent of linkage disequilibrium (LD) (physical distance reached for $r^2=0.2$ according to Hill and Weir, (1988)) on the corresponding chromosome (mean linkage disequilibrium decay of 2.2 kb, as described in Blois et al. (submitted)). This procedure made it possible to obtain genes linked to all significant markers except chr5_19758975. In this case, the two flanking genes of the marker region were considered. Gene functions were defined according to information available from UniProt (The UniProt Consortium 2021).

4.4 Results

Genetic variability of root-related traits

Phenotypic variability was observed for root traits in the *V. berlandieri* population in 2020 and 2021 (Figure 1). RDW was higher in 2021 than in 2020; Tot_Root_NB, Tot_Diam, and the number roots in each size class were lower in 2021 than in 2020 (Table S 4.2). RDW ranged from 0.4 g to 10.9 g in 2020 and from 0.1 g to 16.7 g in 2021, with a higher mean in 2021 than

in 2020 (35% lower in 2020) (Table S 4.1). PW, SD and RSD were very similar over the two years of experiment, with a mean PW of 27.6 g and 27.0 g, a mean SD of 4.9 mm and a mean RSD_1/RSD_2 of 7.2/8.4 mm and 7.3/8.3 mm in 2020 and 2021 respectively. Tot_Root_NB in the *V. berlandieri* population was 32% higher in 2020 (mean = 17.2) than in 2021 (mean = 13.0). Mean Tot_Diam was higher in 2020 (26.4 mm) than in 2021 (19.6 mm), but mean Av_Diam was similar in 2021 (1.7 mm) and 2020 (1.6 mm). The numbers of roots in each size class were greater in 2020 than in 2021 with mean values of 5.1, 7.6, and 4.5 for the number of small, medium-sized and large roots, respectively, in 2020 and 4.4, 5.0, and 3.6 for the numbers of small, medium-sized and large roots, respectively, in 2021. The additional roots observed in 2020 were evenly distributed between the three diameter-based classes (*small*, *medium-sized* and *large*), with the same proportion for each class of roots in the two years of measurement (0.3, 0.4 and 0.3 for small, medium-sized and large roots, respectively).

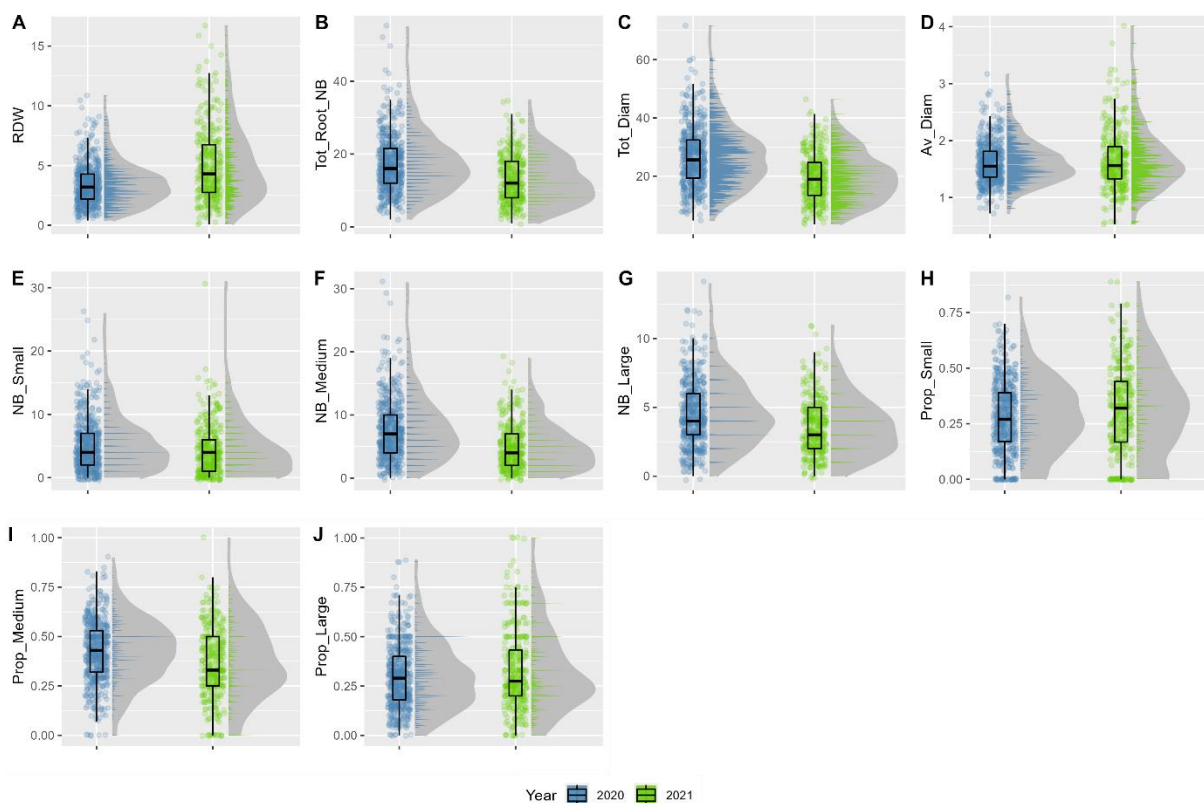


Figure 4.1 : Bocplot and distributions of root-related traits measured in 2020 (blue) and 2021 (green). For each trait, a boxplot is shown on the left and a bar plot distribution on the right, with a density curve indicated in gray. The density curve was calculated with the `stat_lab` function of the `ggdist` package in R with an adjustment of 0.01. The traits shown are root dry weight (RDW, A), total root number (Tot_Root_NB, B), total diameter (Tot_Diam, C), mean diameter (Av_Diam, D), the number of small roots (NB_Small, diameter < 1 mm, E), the number of medium-sized roots (NB_Medium, 1 mm < diameter < 2 mm, F), the number of large roots (NB_Large, diameter > 2 mm, G), the proportion of small roots (Prop_Small, H), the proportion of medium-sized roots (Prop_Medium, I), and the proportion of large roots (Prop_Large, J).

The genetic coefficient of variation (CVg) was high, except for traits not related to genetic performance (SD and RSD). Excluding SD and RSD, CVg ranged from 0.15 for the proportion of *medium-sized* roots to 0.45 for the number of *medium-sized* roots (Table 4.1). For all traits, heritability was moderate to high, ranging from 0.36 for the proportion of *medium-sized* roots to 0.82 for the number of roots.

Table 4.1: Summary of root traits in 2020 and 2021 (H^2 is the broad-sens heritability of traits for the two years of the experiment calculated from genetic models, CVg is the coefficient of variation based on BLUP values from the same model)

	H^2	CVg	Min	Max	Mean	St Dev
RDW	0.71	0.34	0.1	16.7	4.0	2.5
SD	0.45	0.06	2.3	7.3	4.7	0.7
RSD_1	0.53	0.04	5.0	11.2	7.3	0.9
RSD_2	0.62	0.04	5.9	11.8	8.3	1.0
Tot_Root_NB	0.82	0.32	1.0	55.0	15.6	7.6
Tot_Diam (mm)	0.73	0.22	1.4	71.7	23.3	9.5
Av_Diam (mm)	0.47	0.21	0.3	10.0	1.7	0.9
NB_Small	0.61	0.44	0	31.0	4.9	4.1
NB_Medium	0.79	0.45	0	31.0	6.6	4.5
NB_Large	0.56	0.25	0	14.0	4.2	2.3
Prop_Small	0.48	0.27	0	0.9	0.3	0.2
Prop_Medium	0.36	0.15	0	1.0	0.4	0.2
Pop_Large	0.64	0.32	0	1.0	0.3	0.2

The variables were organized similarly in 2020 and 2021 and the first two principal components explained 80% of the variability of traits (Table 4.2). RDW and the number of large roots were correlated, as were RN and the number of medium-sized roots. The panel of genotypes studied was not identical for the two years. It was therefore very difficult to compare individual coordinates. However, a small number of genotypes with more extreme coordinates, close to those of commercial rootstocks, are labeled on Figure 4.3A and Figure 4.3B. The same three genotypes (26186, 25436, 24894) were labeled in both years and had similar coordinates in both years.

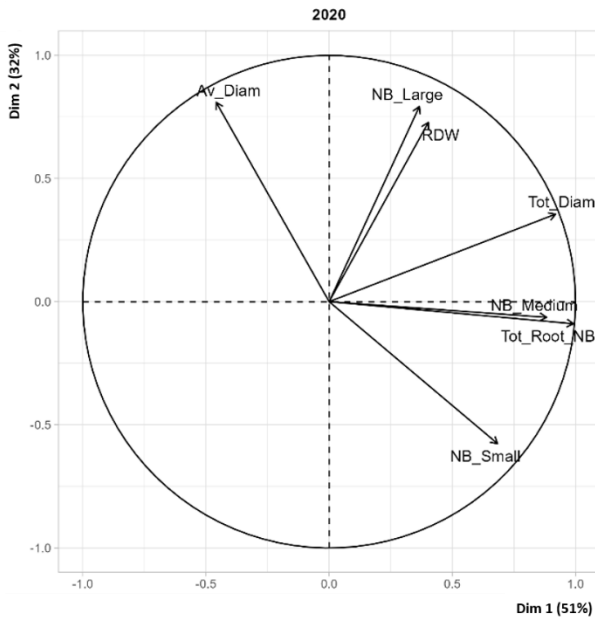
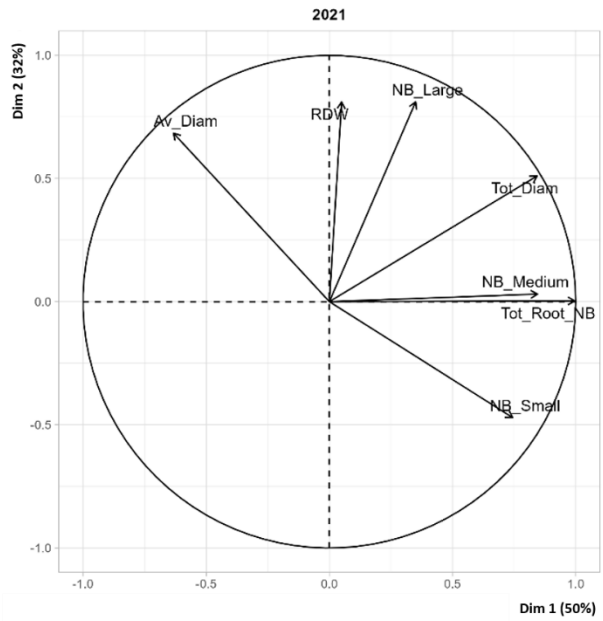
A**B**

Figure 4.2 : Graph of variables obtained from the PCA analyses in 2020 (A) and 2021 (B). Commercial rootstock performances were not considered for the calculation of coordinates.

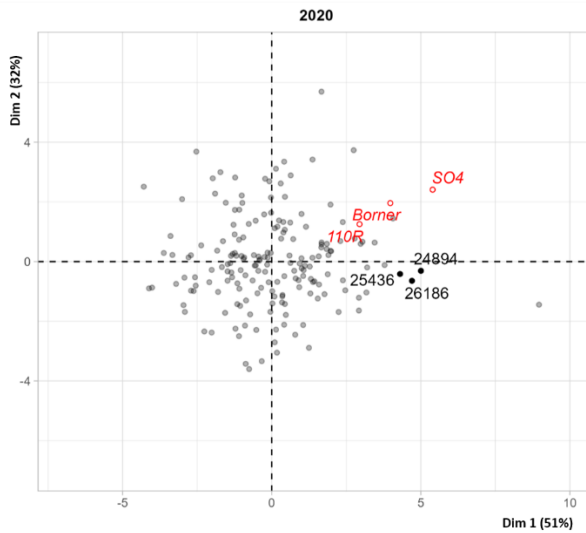
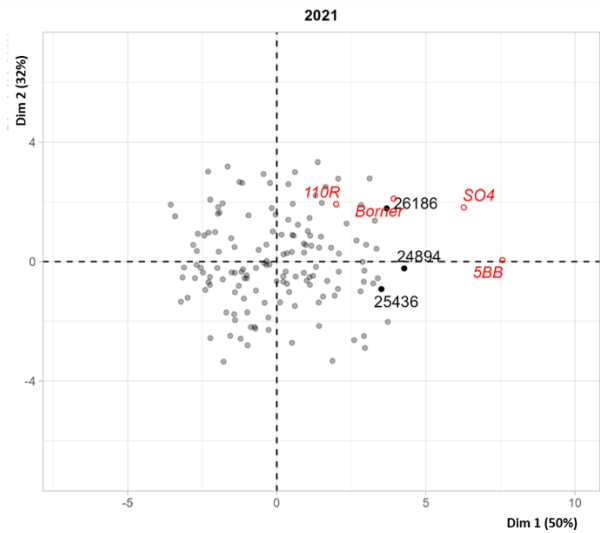
A**B**

Figure 4.3 : Graph of individuals obtained from the PCA analyses in 2020 (A) and 2021 (B). Commercial rootstocks (110R, Börner, 5BB, and SO4) are indicated in red as additional individuals. Number 24894, 25436 and 26186 indicate individuals with extreme performances for root-related traits similar to those of commercial rootstocks over the two years of the experiment.

PW, SD and RSD depended on shoot sampling before grafting, but significant correlations were observed between plant weight and all root-related traits other than the proportions of each class of root (Figure 4.4). Positive correlations were observed between Tot_Root_NB and all traits other than Av_Diam and Prop_Large (inversely correlated with Tot_Root_NB). Av_Diam and Prop_Large were inversely correlated with all root-related traits.

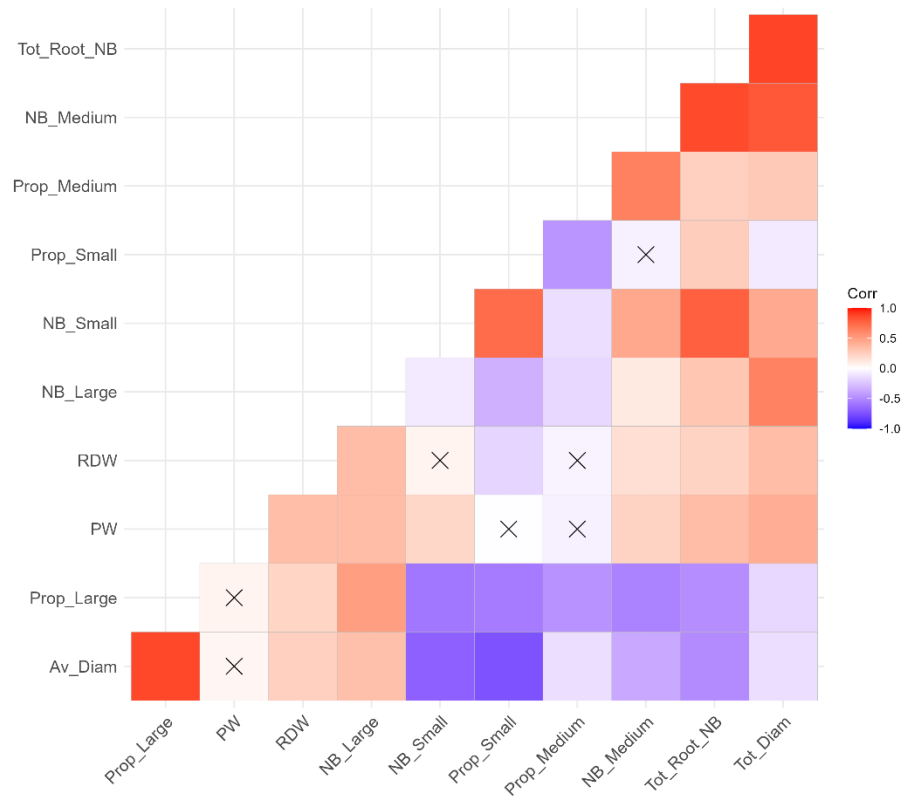


Figure 4.4 : Correlation matrix for root-related traits, based on Pearson correlation matrix for all root-related traits. Crosses indicate a non-significant correlation and the color indicates the nature of the correlation, with positive correlations shown in red and inverse correlations in blue. The intensity of the hue indicates the strength of the correlation.

GWAS on root-related traits

The BLUE values were used as phenotypic values for GWAS. Plant weight, year of experimentation and genotype had significant effects in the model for all traits except plant weight for Prop_Medium (Table S 4.3). GWAS identified 11 markers associated with the Av_Diam of roots (located on chromosomes 8, 10, 17, and 18), Tot_Root_NB (chromosome 5), NB_Small (chromosomes 1, 9, 13, and 17), and NB_Medium (chromosomes 5 and 14) (Table 4.2). These markers explained between 0.4% and 25.1% of the trait variance. The chr5_19758975 marker was identified for two traits: Tot_Root_NB and NB_Medium.

Table 4.2 : Significant marker list (Chr indicates the chromosome, Effect is the intercept calculated in BLINK using the marker as a fixed effect in a linear model, r^2 was calculated in BLINK using the marker as a random effect in a linear model, Maf is the minor allele frequency ; genes were obtained with the annotated sequence of *V. berlandieri*, and functions were suggested in UniProt)

Chr	Position	Trait	Effect	r^2 (%)	Maf	P-value	Size (bp)	Gene	Function	Source
chr8	3205879	Average diameter	-0.5	1.7	0.27	1.64E-07	6606	Vitvi08g02318	PREDICTED: UPF0481 protein At3g47200-like Integral component of membrane	IEA:UniProtKB-KW
chr10	24863208	Average diameter	2.1	25.1	0.06	2.45E-16	2902	Vitvi10g02297	Unknown	
chr17	4986873	Average diameter	0.2	0.9	0.38	5.55E-07	2356	Vitvi17g00422	Stricosidine synthase	IEA:EnsemblPlants
chr18	13881469	Average diameter	1.9	1.8	0.25	5.96E-08	9876	Vitvi19g00545; Vitvi18g01271; Vitvi18g01272; Vitvi18g01273	Unknown	
chr5	19758975	Total root number	-0.3	0.4	0.12	1.79E-08	855	Vitvi05g01219; Vitvi05g02076	GTPase activity; unknown	IBA:GO_Central
chr1	2250037	Number of small roots	0.1	1.4	0.11	6.44E-10	7808	Vitvi01g01633; Vitvi01g01632; Vitvi01g01631	Unknown	
chr9	18214759	Number of small roots	0	0.6	0.06	3.78E-11	860	Vitvi09g00521	Metal ion binding	IEA:EnsemblPlants
chr13	8270412	Number of small roots	-7	1.0	0.14	9.03E-12	1068	Vitvi13g00728	UMP kinase activity	IBA:GO_Central
chr17	4296526	Number of small roots	0.9	8.5	0.17	1.49E-10	2356	Vitvi17g00360; Vitvi17g00361	Transcription regulator; unknown	IBA:GO_Central
chr5	19758975	Number of medium-sized roots	-0.6	4.3	0.12	4.85E-08	855	Vitvi05g01219; Vitvi05g02076	GTPase activity; unknown	IBA:GO_Central
chr14	21295561	Number of medium-sized roots	-2.5	6.0	0.09	1.28E-07	1852	Vitvi14g01232	Nuclear organization	IEA:EnsemblPlants

The chr8_3205879 and chr17_4986873 markers were significant for the Av_Diam (Figure 4.5) and explained 1.7% and 0.9% of the trait variance, respectively. The other two significant markers, chr10_24863208 and chr18_13881469, explained 25.1% and 1.8% of the trait variance, respectively. The chr8_3205879 marker was linked to the Vitvi08g02318 gene, chr10_24863208 was linked to Vitvi10g02297, chr17_4986873 was linked to Vitvi17g00422, and chr18_13881469 was linked to Vitvi19g00545, Vitvi18g01271, Vitvi18g01272, and Vitvi18g01273 (Table 4.2).

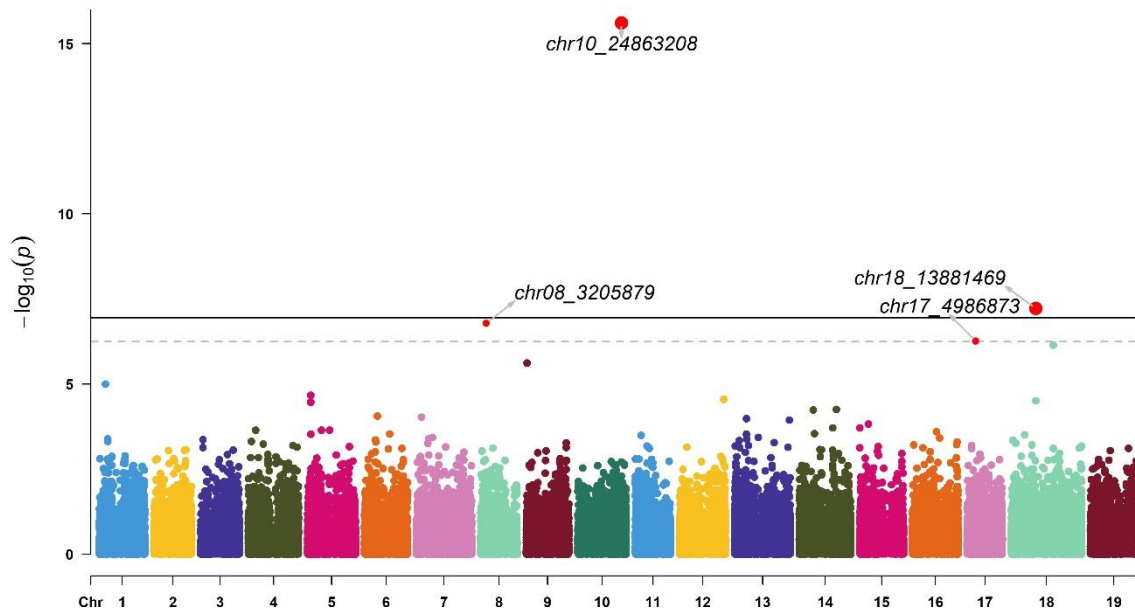


Figure 4.5 : Manhattan plot for SNP associations with mean root diameter (*Av_Diam*). The thresholds were calculated with the Bonferroni method for $\alpha = 0.05$ (dashed line) and 0.01 (solid line). Significant signals are indicated by a small red dot for $\alpha = 0.05$ and a larger red dot for $\alpha = 0.01$. The corresponding QQ plot is presented in Figure S 4.3A)

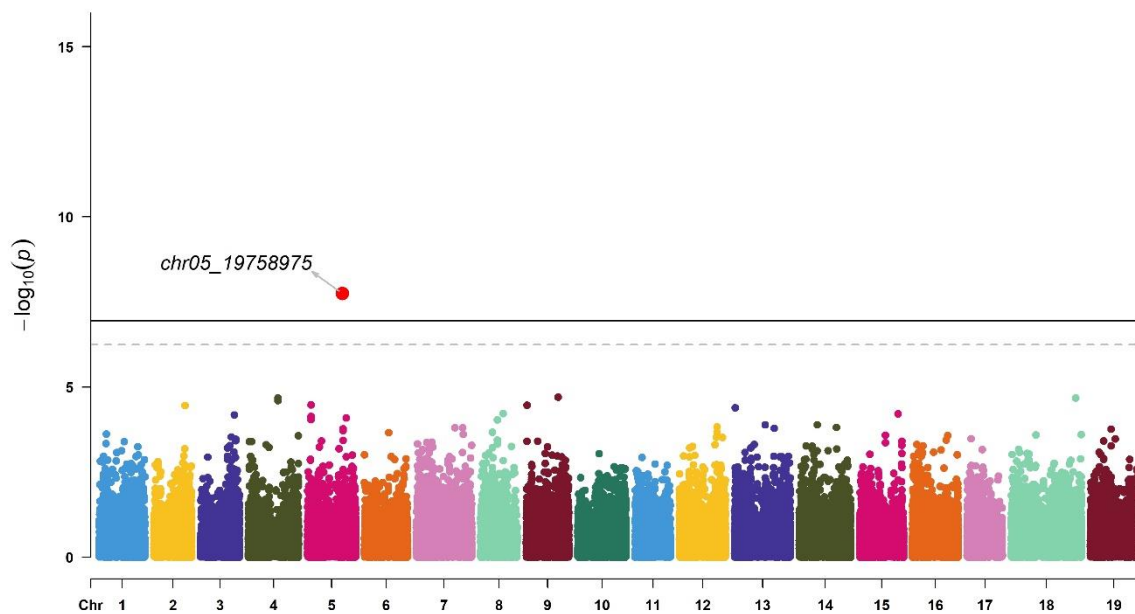


Figure 4.6 : Manhattan plot for SNP associations with total root number (*Tot_Root_NB*). The thresholds were calculated with the Bonferroni method for $\alpha = 0.05$ (dashed line) and 0.01 (solid line). Significant signals are indicated by a small red dot for $\alpha = 0.05$ and a larger red dot for $\alpha = 0.01$. The corresponding QQ plot is presented in Figure S 4.3B)

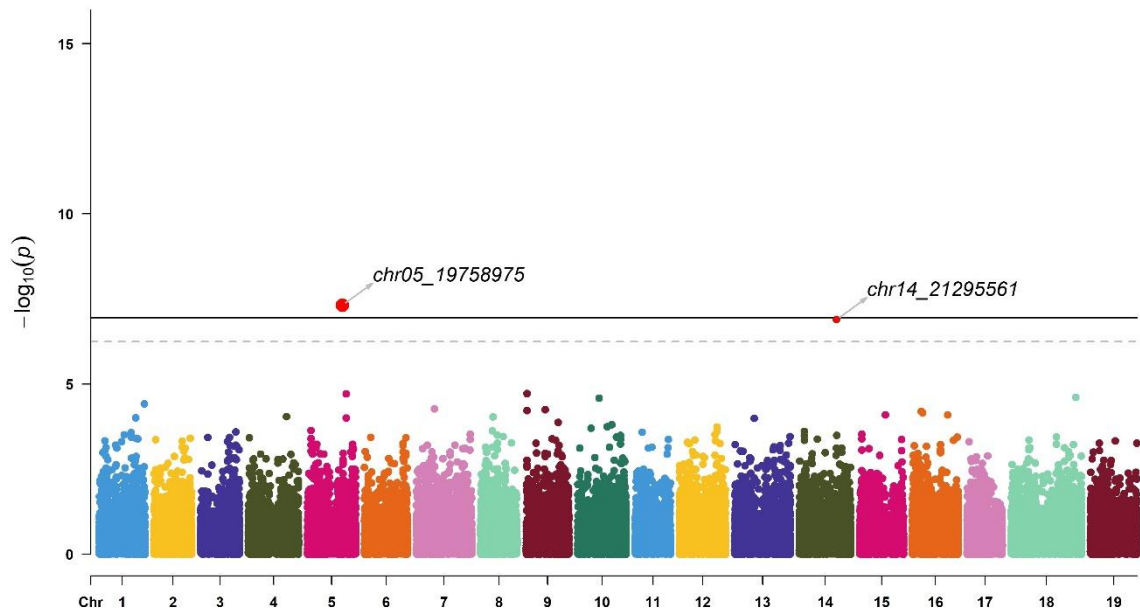


Figure 4.7 : Manhattan plot for SNP associations with the number of medium roots (NB_Medium, diameter from 1 mm to 2 mm). The thresholds were calculated with the Bonferroni method for $\alpha = 0.05$ (dashed line) and 0.01 (solid line). Significant signals are indicated by a small red dot for $\alpha = 0.05$ and a larger red dot for $\alpha = 0.01$. The corresponding QQ plot is presented in Figure S 4.3D)

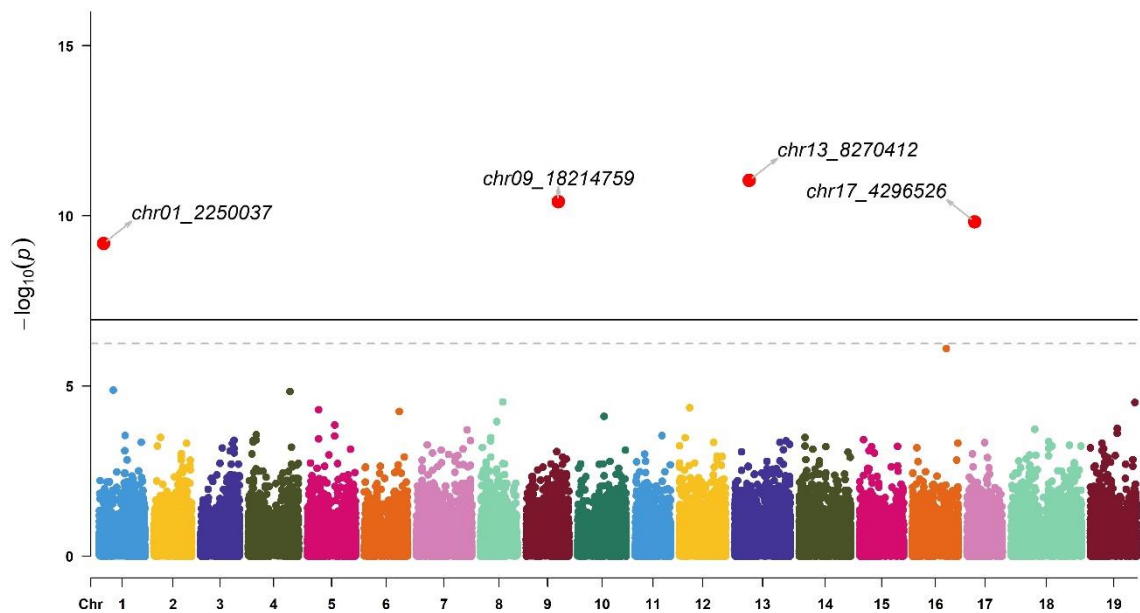


Figure 4.8 : Manhattan plot for SNP associations with the number of small roots (NB_Small, diameter < 1 mm). The thresholds were calculated with the Bonferroni method for $\alpha = 0.05$ (dashed line) and 0.01 (solid line). Significant signals are indicated by a small red dot for $\alpha = 0.05$ and a larger red dot for $\alpha = 0.01$. The corresponding QQ plot is presented in Figure S 4.3C.

One marker, chr5_19758975, was identified as significant for both Tot_Root_NB (Figure 4.6; Table 4.2) and NB_Medium (Figure 4.7), explaining 0.4% and 4.3% of the variance, respectively, for these traits. It was linked to the genes Vitvi05g01219 and Vitvi05g02076 (Table 4.2). The chr14_21295561 marker was also found to be significant for NB_Medium, accounting for 6.0% of the variance for this trait and linked to the Vitvi14g01232 gene (Table 4.2).

NB_Small was significantly associated with chr1_2250037, chr9_18214759, chr13_8270412, and chr17_4296526 (Figure 4.8; Table 4.2) with $r^2 = 1.4\%$, 0.6% , 1.0% , and 8.5% , respectively. The chr1_2250037 marker was linked to Vitvi01g01633, Vitvi01g01632, and Vitvi01g01631 (Table 4.2). The chr9_18214759 marker was linked to Vitvi09g00521, chr13_8270412 was linked to Vitvi13g00728, and chr17_4296526 was linked to Vitvi17g00360 and Vitvi17g00361 (Table 4.2). For each marker, we explored the effects of each allele in the homozygous and heterozygous states (Figure 4.9).

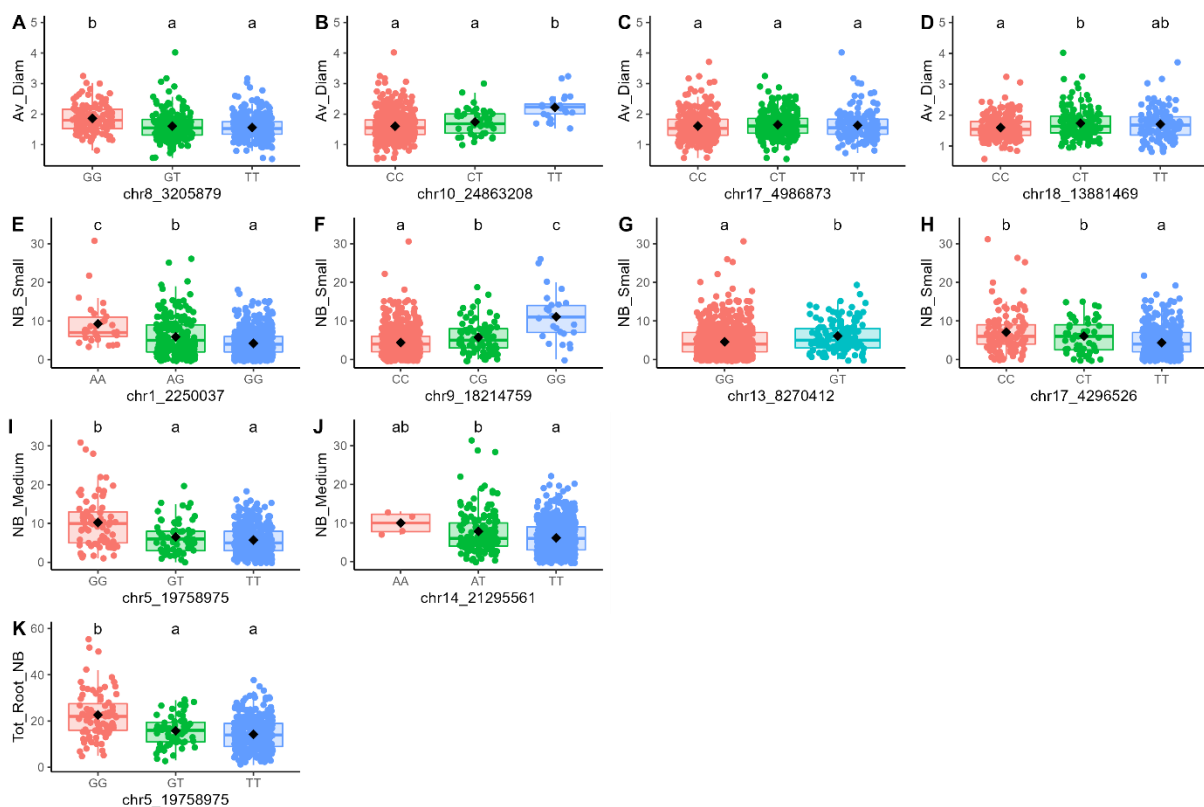


Figure 4.9 : Boplots of marker effects on root-related traits : chr17_4986873 (A), chr8_3205879 (B), chr10_24863208 (C), and chr18_13881469 (D) for mean root diameter (Av_Diam); chr5_19758975 (E) for total root number (Tot_Root_NB), chr1_2250037 (F), chr13_8270412 (G), chr17_4296526 (H), and chr9_18214759 (I) for the number of small roots (NB_Small, diameter < 1 mm), and chr14_21295561 (J) and chr5_19758975 (K) for the number of medium roots (NB_Medium, 1 mm > diameter < 2 mm).

Root-related trait performances

Commercial rootstocks are widely used in vineyards and were used as controls for favorable root-related traits in comparisons with *V. berlandieri* genotypes. The commercial rootstocks had higher RDW, RN and RTD values than the *V. berlandieri* genotypes. However, a few *V. berlandieri* genotypes had similar values to the commercial rootstocks for these traits in both years (Figure S 4.1). Commercial rootstocks displayed greater variability for RDW, Tot_Root_NB, Av_Diam, NB_Small, and NB_Medium in 2021 than in 2020 (Table S 4.1), probably due to the addition of genotype 5BB to the pool for the second year of the experiment. However, Tot_Diam variability was lower in 2021. Commercial rootstocks performed well, with high values of RDW, Tot_Root_NB, and Tot_Diam, over the two years of experiment (Figure S 4.1 and Figure S 4.2).

The commercial rootstocks (used as additional individuals) had similar coordinates in the two years, with 110R and Börner located close together on the graph (Figure 4.3). 5BB was present only in the 2021 panel and can be distinguished by its high Tot_Root_NB. The 26186, 25436, and 24894 genotypes stood out on the individual PCA graph (Figure 4.3) because they had similar extreme coordinates to the controls on the PCA, in both years of the experiment.

4.5 Discussion

A wild *Vitis* population (*V. berlandieri*) relevant for rootstock breeding was evaluated with two independent sets of plants for root-system phenotypes after grafting with the Riesling variety. This population displayed considerable genetic variability for root-related traits. We also performed a GWAS for root-related traits on the *V. berlandieri* population. Significant QTLs were identified for four root-related traits: four for mean diameter, with one marker explaining 25.1% of the trait variance, one for the total number of roots, four for the number of *small* roots, with one marker explaining 8.5% of the trait variance, and two for the number of *medium* roots. We then compared the root-system profiles of the *V. berlandieri* population with those of commercial rootstocks, to identify promising genotypes for breeding.

Genetic variability of root-related traits

Root system architecture is of considerable importance, given its contribution to plant productivity and adaptation. However, plant root systems are difficult to phenotype, resulting

in a larger number of studies for annual crops, which have smaller root systems, than for perennials. Root traits have been shown to have a moderate-to-high heritability and coefficient of variation in cotton (Cui et al. 2022) and in several cereal crops, including maize seedlings (Pace et al. 2015; Sanchez et al. 2018), barley (Reinert et al. 2016; Abdel-Ghani et al. 2019), and rice (Courtois et al. 2013; Biscarini et al. 2016; Phung et al. 2016).

Our results were consistent with these previous studies. Root diameter and root number were highly variable and had a moderate-to-high heritability. Tandonnet et al. (2018) obtained similar results for grapevine root section (related to root diameter) and root number ($H^2=0.64$ and 0.7 respectively) in a *V. vinifera* cv. Cabernet-Sauvignon \times *V. riparia* cv. Gloire de Montpellier progeny. Root diameter is related to root function, with thicker roots more involved in transport and storage and representing a long-term investment for the plant (Comas, Bauerle, and Eissenstat 2010). In rice, thick roots established before drought stress events improve the drought tolerance of the plants (Price and Courtois 1999; Gowda et al. 2011). Conversely, fine roots are involved in the absorption of water and nutrients and represent a short-term investment for the plant. Moreover, root diameter is also related to root hydraulic conductivity (Rieger and Litvin 1999) and mycorrhization capacity (Peat and Fitter 1993), which can affect plant physiology, production and adaptation (Smith and Read 2010). The genetic variability observed for root-related traits in the *V. berlandieri* population may, thus, be correlated with other traits of interest, such as those mentioned above.

In this study, the root system developed from a piece of wood (after grafting), leading to a homorhizic root system architecture composed of adventitious roots initiated from the node of the rootstock. Each root beginning at the node is considered to be a primary root. We studied plants growing on a homogeneous substrate in pots, to limit the impact of soil chemical and physical variability on the growth and development of the root system (Seguin 1972). However, this made it difficult to study root architecture traits, such as angles, density and length. The moderate-to-high variability and heritability of root-related traits observed in this study suggested that it would be worth performing a GWAS for these traits.

GWAS for root-related traits

We used the BLINK (Bayesian information and linkage disequilibrium iteratively nested keyway) model, which has been shown to have the best performance for detecting significant markers in GWAS (Huang et al. 2018).

Root systems have mostly been studied in annual crops, and GWAS has identified markers involved in the determinism of root-related traits principally in cereals, such as maize (Hochholdinger and Tuberosa 2009; Pace et al. 2015; Zaidi et al. 2016; Bray and Topp 2018; Sanchez et al. 2018; Zheng et al. 2020), rice (Courtois et al. 2013; Biscarini et al. 2016; Phung et al. 2016; Kadam et al. 2017; Li et al. 2017; Zhao et al. 2018), wheat (Ayalew et al. 2018; Alahmad et al. 2019; Beyer et al. 2019) and barley (Reinert et al. 2016; Abdel-Ghani et al. 2019). To our knowledge, no previous study has ever been performed on woody perennial grafted plants.

Our GWAS identified 11 markers associated with root-related traits explaining 0.4% to 25.1% of the variance for individual traits. The proportion of the variance explained by the detected markers was higher in this study than previously reported for cereal crops. Most of the markers were linked to genes of unknown function (Table 4.2), particularly those explaining more than 25% of the variance for mean diameter. However, chr5_19758975, a marker identified for the total number of roots and the number of medium-sized roots, was linked to Vitvi05g01219, encoding a protein potentially involved in GTPase activity. The chr8_3205879 marker associated with mean diameter was predicted to associated with a gene encoding a protein resembling At3g47200 (Dunkley et al. 2006), which is an integral membrane component. The chr9_18214759 marker was linked to the Vitvi09g00521 gene potentially involved in metal ion binding (Johnson et al. 2005), potentially accounting for the limestone tolerance of the *V. berlandieri* genetic background. The chr13_8270412 marker was linked to the Vitvi13g00728 gene encoding a protein with UMP kinase activity. The chr14_21295561 marker was linked to the Vitvi14g01232 gene involved in nuclear organization (Sajiki et al. 2009). The markers detected on chromosome 17 (chr17_4296526 associated with NB_Small and chr17_4986873 associated with Av_Diam) were linked to the genes Vitvi17g00360 and Vitvi17g00422, respectively. Vitvi17g00360 encodes a transcription regulator, whereas Vitvi17g00422 encodes a protein potentially involved in strictosidine synthesis, which is involved in more than 1000 indole alkaloid pathways (Kutchan 1993). Alkaloids are involved

in plant protection against diverse pressures and are present at high concentrations in flowering plants (Sumner, Mendes, and Dixon 2003). They act as defense chemicals in *Catharanthus roseus* (Luijendijk, van der Meijden, and Verpoorte 1996) and are involved in various pathways in *Arabidopsis thaliana* (defense, drugs for human diseases) (Kibble et al. 2009). One quantitative genetic study carried out on a *Vitis vinifera* cv. Cabernet-Sauvignon × *V. riparia* cv. Gloire de Montpellier progeny based on 212 microsatellite markers has revealed genetic regions correlated with root-related traits (Tandonnet et al. 2018). Similarly to our results, QTL were found on linkage groups 5 and 9 but the large confidence intervals of these markers (40 to 56 cM) made it difficult to compare with our results.

Blois et al. (submitted) detected markers associated with environmental variability in the same wild *V. berlandieri* population. Given the short LD decay observed (2.2 kb) in the population, these markers were probably not linked to the markers detected in this study. However, the functions of the genes potentially linked to significant markers were similar. For instance, the chr09_18214759 (this study) and chr07_3341495 (Blois et al. (submitted)) markers were linked respectively to the Vitvi09g00521 and Vitvi01g01826 genes, both of which encode proteins involved in metal ion binding. Moreover, the chr15_1889550 marker was linked to the Vitvi15g01070 gene encoding a protein involved in the iron pathway. These genes should be explored in greater depth, because they may account for the outstanding limestone tolerance observed in this species (Galet 1988).

Given the role of the root system in plant productivity and stress tolerance (Meister et al. 2014; Maqbool et al. 2022), the markers explaining a large proportion of trait variance ($r^2 = 25.1\%$ on chr10_24863208 for Av_Diam and $r^2 = 8.5\%$ on chr17_4296526 for NB_Small,) should be investigated in greater depth (in a quantitative genetic study with a pedigree population, for example) with a view to inclusion in grapevine rootstock breeding programs.

Root-related trait performances

In grafted cultivated plants, such as fruit trees, grapevine, and other species, including tomatoes, the root system genotype differs from the scion genotype. It is therefore possible to improve the root system of the plant directly, improving the biotic and abiotic tolerance of the plant, without the need to modify the scion (Marguerit et al. 2012; Tamura 2012).

The commercial rootstocks used have been reported to confer vigor on the scion, together with tolerance to drought, limestone and phylloxera, all of which are parameters of interest for grapevine rootstocks. Root-system profiles have a strong impact on drought tolerance and nutrient capture (Lynch 1995). The drought tolerance of commercial rootstocks is considered very high for 110R, high for Börner, moderate-to-high for SO4 and low for 5BB. The relationships between root-related traits and drought tolerance require further exploration. The selection of root-system traits of interest is complex, because it depends on environmental conditions, soil properties, plant species, and cultural practices (Lynch 2018). Ideotypes are then explored to identify the root-system profiles suitable for the broadest range of environmental conditions. The *steep*, *cheap* and *deep* root-system profile has been proposed by Lynch, (2013), in which roots grow deeply but with the lowest “carbon cost” possible. However, this profile was proposed for annual crops, and ideotypes may be very different for perennials, in which the target may also be to invest more carbon in root-system growth and development so as to obtain a well-established root system. This would enable the plant to increase the volume of soil explored and to gain access to more water resources in conditions of water deficit. Given the difficulty of selecting root-system ideotypes, we based our performance criteria on the root-system profiles of commercial rootstocks, which had large numbers of roots of evenly balanced diameters, resulting in high total root diameters. The widespread use of these commercial rootstocks reflects their good performance in the field. We therefore assumed that they perform better than other rootstocks in the field due to their specific root-system profiles. Then, *V. berlandieri* genotypes with root-system profiles similar to those of commercial rootstocks (24894, 25436 and 26186) therefore constitute promising candidates for use as parental material in breeding programs. It should also be borne in mind that we measured root traits at a juvenile stage (1 year), and that these traits might not be maintained at later stages in this perennial plant. Rootstocks can have a major effect on the physiological processes in scions (Gregory et al. 2013). It is, therefore, very important to test these genotypes in the grafted state in field conditions, to characterize their tolerances to limestone and drought.

4.6 Conclusion

Our results highlight the considerable genetic variability of root-related traits in a wild *V. berlandieri* population and the moderate-to-high heritability of these traits. Moreover, we performed a genome-wide association study for root-related traits, which identified 11 markers associated with these traits. Two of these markers explained a large proportion of the trait variance, suggesting that they could be used in marker-assisted selection, to facilitate the breeding of improved rootstocks. A few wild genotypes had performances similar to those of widely used commercial rootstocks. However, these genotypes would need to be characterized for the other agronomic traits important in grapevine rootstocks, such as drought tolerance, tolerance to limestone and vigor in field conditions. The genotypes identified may be outstanding candidates for use in breeding, and a field experiment is currently being set up in Bordeaux to assess their agronomic performances.

4.7 Acknowledgement

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4.9 Supplemental data

Table S 4.1 : Number of replicates in the population grafted in 2020 and 2021.

	2020	2021
1 replicate	47	63
2 replicates	38	34
3 replicates	33	23
4 replicates	27	14
5 replicates	36	10
Total	181	144

Table S 4.2 : General root statistics for the *V. berlandieri* population

	2020				2021			
	Min	Max	Mean	StDev	Min	Max	Mean	StDev
RDW (g)	0.4	10.9	3.4	1.7	0.1	16.7	5.0	3.1
PW (g)	15.9	47.7	27.6	5.5	15.8	49.5	27.0	5.6
SD (mm)	3.2	7.3	4.9	0.7	2.3	6.7	4.5	0.7
RSD_1 (mm)	5.2	10.6	7.2	0.9	5.0	11.2	7.3	0.9
RSD_2 (mm)	6.0	11.8	8.4	1.0	5.9	11.6	8.2	0.9
Tot_Root_NB	2.0	55.0	17.2	7.7	1.0	35.0	13.0	6.5
Tot_Diam (mm)	4.8	71.7	26.4	10.1	3.5	46.4	19.6	8.2
Av_Diam (mm)	0.7	3.2	1.6	0.4	0.5	4.0	1.7	0.5
NB_Small	0.0	26.0	5.1	4.1	0.0	31.0	4.4	4.0
NB_Medium	0.0	31.0	7.6	4.7	0.0	19.0	5.0	3.6
NB_Large	0.0	14.0	4.5	2.3	0.0	11.0	3.6	2.1
Prop_Small	0.0	0.8	0.3	0.2	0.0	0.9	0.3	0.2
Prop_Medium	0.0	0.9	0.4	0.2	0.0	1.0	0.4	0.2
Pop_Large	0.0	0.9	0.3	0.2	0.0	1.0	0.3	0.2

Table S 4.3 : Best linear unbiased estimates (BLUE) model output. The significance of the factors used in the BLUE model are indicated in the Pr(>F) column. The factors indicated are the year of the experiment, the plant weight (PW) and the genotype.

Trait	Factor	Pr(>F)
RDW	Year	< 2.2e-16
	PW	< 2.2e-16
	Genotype	< 2.2e-16
Tot_Root_NB	Year	< 2.2e-16
	PW	1.62e-15
	Genotype	< 2.2e-16
Tot_Diam	Year	< 2.2e-16
	PW	< 2.2e-16
	Genotype	< 2.2e-16
Av_Diam	Year	0.01
	PW	4.8e-04
	Genotype	< 2.2e-16
NB_Small	Year	0.02
	PW	0.05
	Genotype	< 2.2e-16
NB_Medium	Year	< 2.2e-16
	PW	3.8e-08
	Genotype	< 2.2e-16
NB_Large	Year	1.7e-07
	PW	3.1e-16
	Genotype	1.2e-14
Prop_Small	Year	0.05
	PW	0.04
	Genotype	9.6e-11
Prop_Medium	Year	1.e-07
	PW	0.6
	Genotype	2.4e-06
Prop_Large	Year	5.9e-04
	PW	5.1e-03
	Genotype	< 2.2e-16

Table S 4.4 : General root trait statistic for commercial rootstocks (110R, SO4 and Börner in 2020 and 2021, with 5BB added to the pool in 2021).

	2020				2021			
	Min	Max	Mean	StDev	Min	Max	Mean	StDev
RDW (g)	4.3	11.1	6.5	1.8	8.1	16.4	12.7	2.3
PW (g)	34.8	51.7	40.1	4.3	25.0	41.9	34.3	4.5
SD (mm)	4.5	6.7	5.7	0.8	3.9	6.5	5.1	0.7
RSD_1 (mm)	7.7	10.4	9.0	0.8	6.8	9.6	8.3	0.7
RSD_2 (mm)	8.8	11.6	10.1	0.8	8.1	11.5	9.7	0.9
Tot_Root_NB	17.0	45.0	28.6	7.8	16.0	52.0	30.3	10.2
Tot_Diam (mm)	28.5	69.7	45.5	10.8	24.8	49.6	37.2	7.2
Av_Diam (mm)	1.4	1.8	1.6	0.1	0.9	1.8	1.3	0.2
NB_Small	3.0	18.0	7.9	3.6	4.0	28.0	13.2	7.4
NB_Medium	7.0	27.0	13.1	5.1	5.0	24.0	12.7	5.8
NB_Large	4.0	12.0	7.7	2.2	1.0	8.0	4.4	2.1
Prop_Small	0.2	0.4	0.3	0.1	0.1	0.6	0.4	0.1
Prop_Medium	0.4	0.7	0.5	0.1	0.3	0.6	0.4	0.1
Pop_Large	0.1	0.4	0.3	0.1	0.0	0.4	0.2	0.1

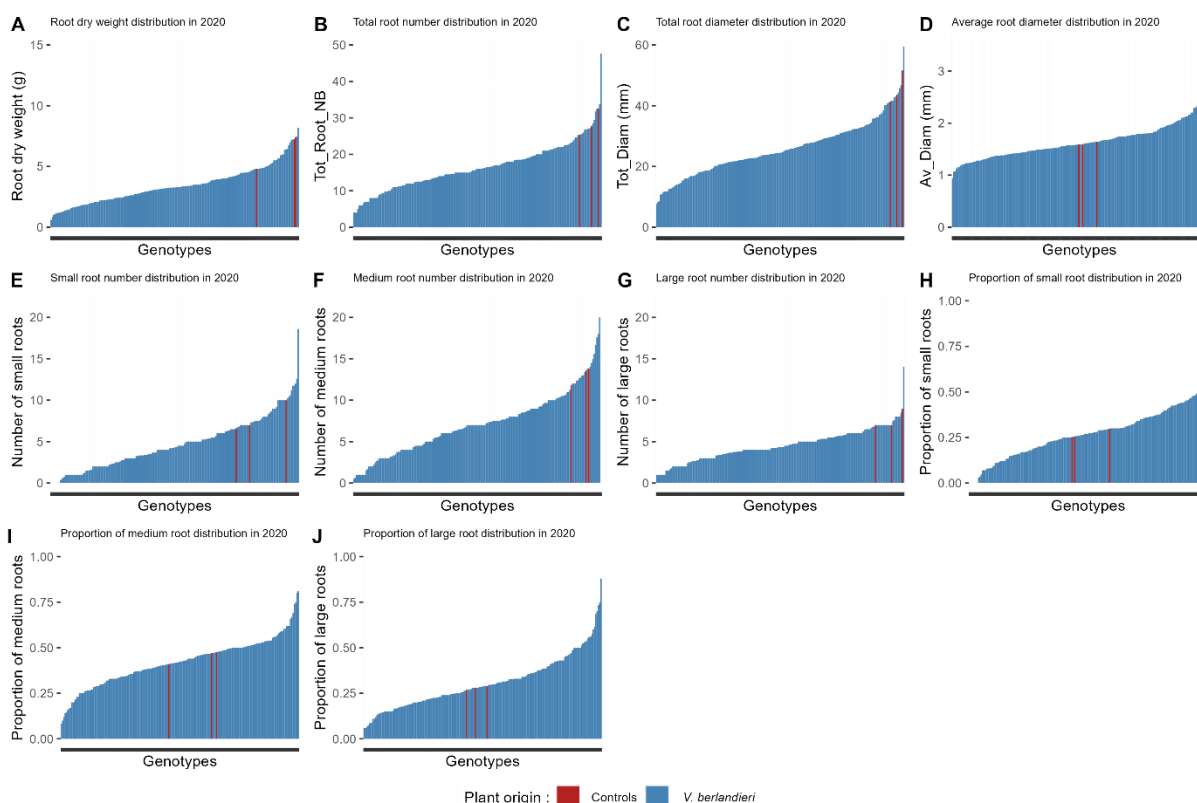


Figure S 4.1 : Distribution of root-related traits measured in 2020. For each trait, red lines indicate the positions of the commercial rootstocks in the distribution (Börner, 110R, and SO4). The traits shown are root dry weight (A), the total number of roots (Tot_Root_NB, B), the total diameter (Tot_Diam, C), the average diameter (Av_Diam, D), the number of small roots (diameter < 1 mm, E), the number of medium roots (1 mm < diameter < 2 mm, F), the number of large roots (diameter > 2 mm, G), the proportion of small roots (H), the proportion of medium roots (I), and the proportion of larger roots (J).

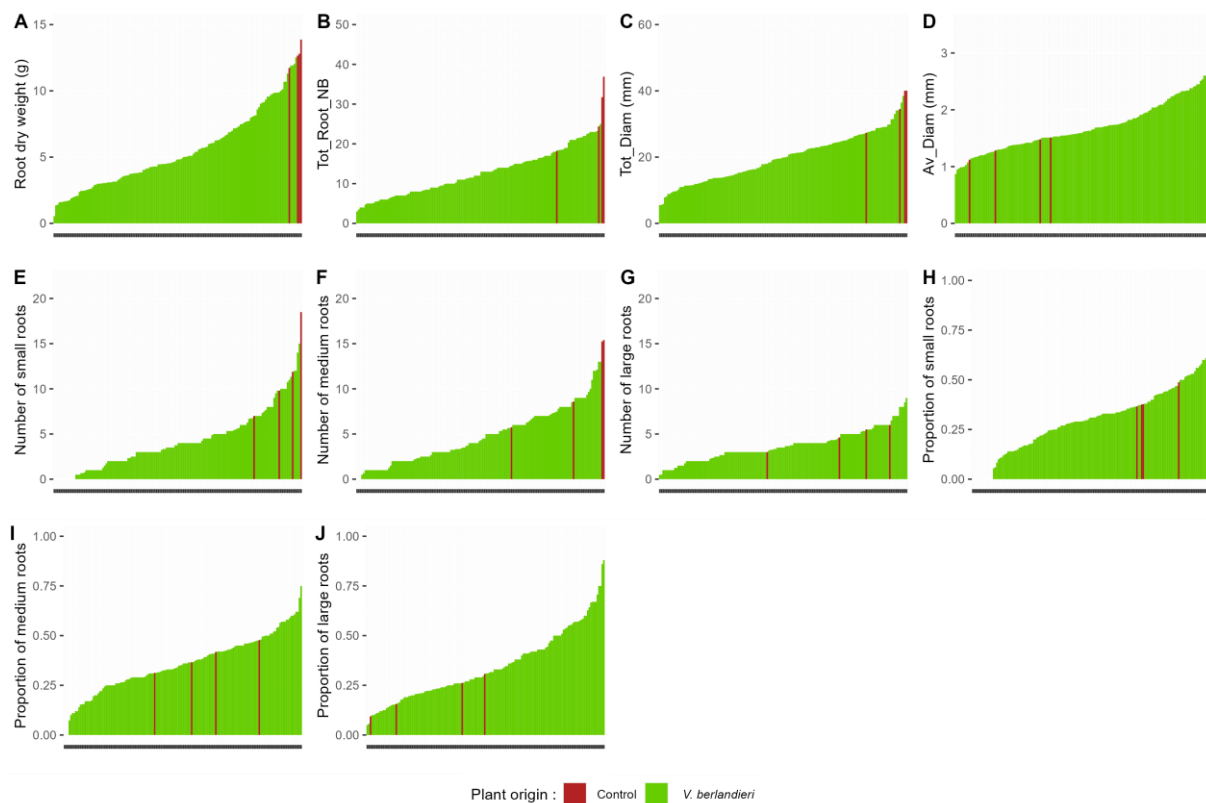


Figure S 4.2 : Distribution of root-related traits measured in 2021. For each trait, red lines indicate the positions of the commercial rootstocks in the distribution (Börner, 110R, and SO4). The traits shown are root dry weight (A), the total number of roots (Tot_Root_NB, B), the total diameter (Tot_Diam, C), the average diameter (Av_Diam, D), the number of small roots (diameter < 1 mm, E), the number of medium roots (1 mm < diameter < 2 mm, F), the number of large roots (diameter > 2 mm, G), the proportion of small roots (H), the proportion of medium roots (I), and the proportion of larger roots (J).

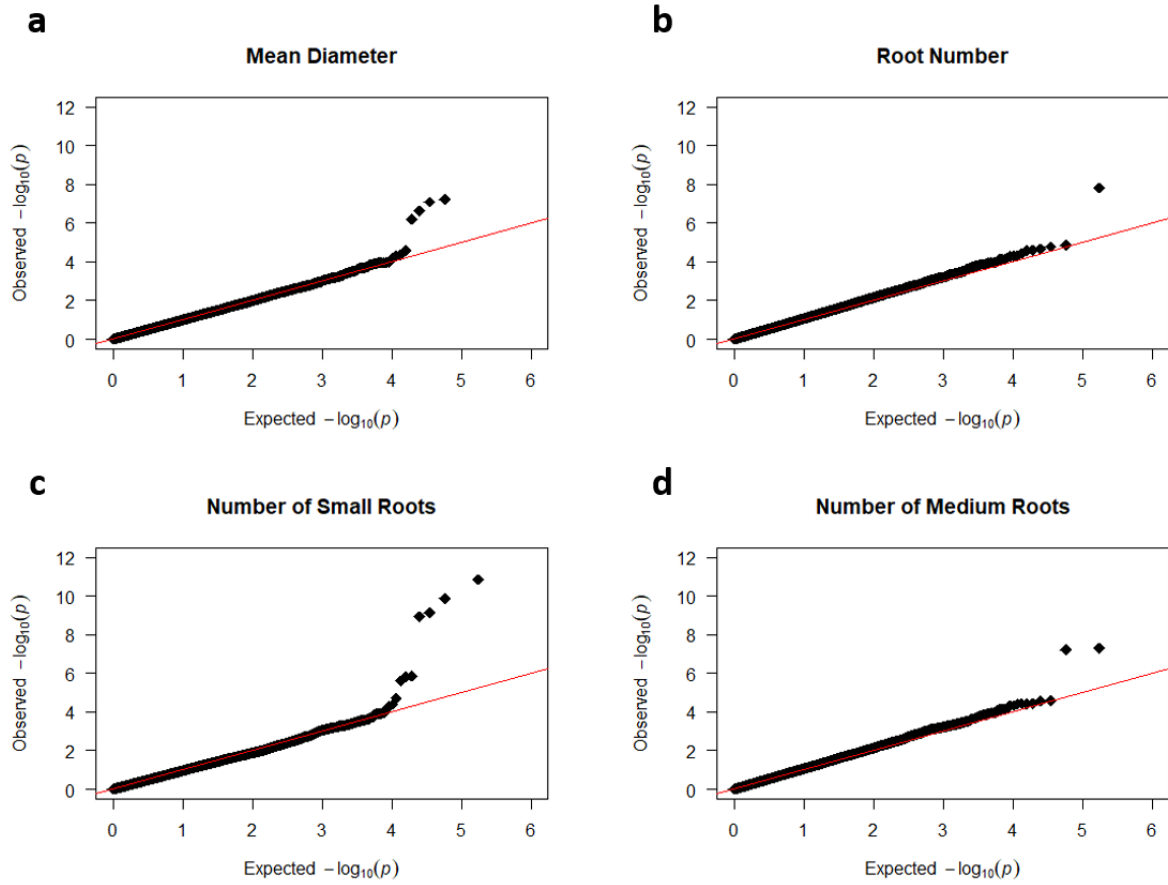


Figure S 4.3 : QQ plot, indicated the distribution of theoretical and observed p -values in the genome-wide association study for root average diameter (A), toele root number (B), the number of small roots (C), and the number of medium roots (D).

Conclusion

This chapter allowed us to observe the variability of root-related traits in the *V. berlandieri* species. The BLUP models allowed to consider the environmental and year of experiment impacts on root-related traits variability to use it as co-variates in order to extract the broad sense heritability of each trait. The heritability and the variability of root-related traits allowed us to find associations of four root-related traits with 11 genetic regions in a GWAS. Because commercial rootstocks used in this study have been selected for their performances in vineyards, it was surprising to find *V. berlandieri* wild genotypes with similar root systems as commercial rootstocks.

This study represents the first root system analysis made on grapevine rootstocks in a grafted context using a single species wild population. It has shown that variability at the phenotypic and genetic level exists in natural conditions, which could be used in grapevine rootstock breeding. These results were consistent with the observations of Péros et al. (2021) who have highlighted the genetic diversity residing inter and intra American grapevine species. Because *V. berlandieri* is a species used as rootstock, it is also of major importance to observe the behavior of a scion grafted with this population.

Chapter 5: Association genetic of
vigor conferred and $\delta^{13}\text{C}$ induced
by grapevine rootstock: first study
in a monospecies population of
Vitis berlandieri

“Whatever you are, be a good one.”

Abraham Lincoln

Introduction

This chapter that will be submitted to *New Phytologist* journal aims to present the results obtained on the scion phenotypic variability when grafted with the *V. berlandieri* population, which are “conferred” traits. We have measured vigor conferred and water use efficiency for two consecutive years in a field experiment. The vigor conferred corresponds to the pruning weight of the plant during the year and the water use efficiency was estimated by $\delta^{13}\text{C}$. We have used BLUP and BLUE models in order to consider the environmental part of the phenotypic variability as well as the year effect. A GWAS have been carried out in order to detect genetic regions associated with the variability of these traits.

Association genetic of vigor conferred and $\delta^{13}\text{C}$ induced by grapevine rootstock: first study in a monospecies population of *Vitis berlandieri*

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5.1 Introduction

Because of climate change, crops adaptation is at the forefront of concerns. Several ways of adaptation are available: cultural practices, field management or plant material selection (van Leeuwen et al. 2019). Considering grafted plants, the adaptation can be achieved thanks to scion or rootstock selection. In grapevine, the scions are issued from *Vitis vinifera* species and have been the focus of breeding for hundreds of years (This, Lacombe, and Thomas 2006). However, more recently because of the phylloxera crisis, grapevines have been cultivated grafted. Thanks to the environmental adaptations and the scion responses induced by rootstocks, they represent an outstanding way of grapevine adaptation (Ollat et al. 2016).

In grapevine rootstock selection, four main targets are considered: the phylloxera tolerance, water deficit and limestone tolerance as well as the vigor conferred to the scion. The variability of plant vigor induced by the rootstock has been observed in tomatoes (Khah et al. 2002; Leonardi and Giuffrida 2006), kiwifruit (Clearwater et al. 2006; Clearwater et al. 2007), apple tree (Costes, Salles, and Garcia 2001; Costes and Garcia-Villanueva 2007) or grapevine (Tandonnet et al. 2018) .

Because of climate change, more intensive and/or frequent water deficit have been predicted in fields in coming years (Giorgi and Lionello 2007). Considering this point, the water use

efficiency (WUE) of plants represents a target for crops adaptation in genetic improvement programs. The WUE could be estimated with the carbon isotope discrimination ($\delta^{13}\text{C}$) (Farquhar and Richards 1984) and allowed to distinguish species for their WUE behaviors. Variations in $\delta^{13}\text{C}$ have been observed when comparing species (*Halimium halimifolium*, *Rosmarinus officinalis*, and *Acacia longifolia*; (Dubbert, Rascher, and Werner 2012), in potatoes accessions (Gouveia et al. 2019), sunflower or perennial ryegrass (Klumpp et al. 2005).

In the context of grafted plants, two genotypes interact at the root system and vegetative part levels. Using this genetic diversity, it is possible to breed directly each one for advantageous traits. Rootstocks are used in plant breeding to modify the scion vigor, precocity, productivity, fruit quality (Webster 1995), and abiotic stress tolerance (Warschefsky et al. 2016).

In grapevine, rootstocks are hybrids between American *Vitis* species (mainly *V. rupestris*, *V. berlandieri*, and *V. riparia*) and sometimes *Vitis vinifera*. Despite the huge diversity observed in American *Vitis* species (Péros et al. 2021), these genetic background remain unexplored yet. Only few genetic studies focused on grapevine rootstocks in a grafted context (Marguerit et al. 2012; Bert et al. 2013; Tandonnet et al. 2018). Genome wide association studies (GWAS) carried out on grapevine have never focused on a specific rootstock species.

The aims of this work were: i) to observe the variability of scion water use efficiency and vigor induced by rootstocks genetics; ii) to carry out GWAS for these conferred traits; iii) compare the performances of these rootstocks with widely used commercial ones; and iv) use previous results obtained for the same population in order to figure out correlations between root-related traits and traits conferred to the scion.

5.2 Materials and Methods

Plant material and field conditions

The plant material was composed by 211 genotypes originated from 72 mother plants of wild *V. berlandieri* (see Blois et al. submitted). These plants were grafted with Riesling (clone 24-209) in 2019 and 2020 in the Grapevine Breeding Department of Geisenheim University, Germany. After one year of growing in pots, the plants were planted in the vineyard of Unité expérimentale Vigne et Vin Bordeaux Grande Ferrade Villenave d'Ornon, in France (44° 47' 32.928" N, 0° 34' 44.468" W). During the experimentation, local weather conditions were recorded with automated weather station.

Plants were planted in 2020 (Experiment1) and 2021 (Experiment2) within six and four rows respectively. Inter rows space was 1.6m and inter stocks was 0.85m. Standard cultural practices were applied during the growing season. The experimental design was composed by seven block in the field based on the number of repetition of each genotype and the soil resistivity variations. In 2020 the blocks one to five were planted and the two last blocks were planted in 2021. In total, the population in composed by 211 genotypes with one to five repetitions per year reaching a total of 823 individuals (183 genotypes in Experiment1 and 142 genotypes in Experiment2). Additionally, commercial rootstocks have been added to the population and spread over the plot. The commercial rootstocks selected were 110R, SO4, Börner and 5BB (only in Experiment2).

Vigor evaluation

Plants were grown with only one shoot. The impact of rootstock on scion vigor was evaluated by the pruning weight measurement at the end of the growing period. It has been measured 17th of March 2021 for the plant vigor of 2020 and the 1st of April 2022 corresponding of the plant vigor of 2021.

Water relations

The impact of rootstocks on the plant water use efficiency was evaluated by $\delta^{13}\text{C}$ measurements. To do so, the number of leaves was counted every 2 or 3 weeks between the start of June and the end of August. Comparing the number of leaves evolution and climatic conditions experienced by plants during the summer, it was possible to select a leaf on each

plant appeared during the same period (end of August for Experiment1 and start of August for Experiment2). The leaf selected have been dried in a dry oven 80°C for 2 weeks. The dried leaves were grinded with a Retsch MM 400. Then, 1mg ± 0.05mg of powder was conditioned in Tin Capsule Pressed (6x4mm) per individual. After combustion in an elemental analyzer (SILVATECH platform of the UMR SILVA, INRAE, Champenoux, France), the carbon isotope composition was analyzed with a CO₂ isotope mass spectrometry analyzer, and expressed as described by Craig (1957):

$$\delta^{13}C (\text{‰}) = \left[\frac{R_{sample}}{R_{std}} - 1 \right] \times 1000 \quad (1)$$

Where R_{sample} and R_{std} are the ratio $^{13}C:^{12}C$ of the sample and the standard respectively. Moreover, pre-dawn leaf water potential (ψ_{pd}) was measured during the driest period experienced in the field over the summer time. Measurements were acquired with a Scholander-type pressure chamber. This measurement was done on different genotypes spread in the experimental plots in order to access the overall plant water status in the field.

Statistical analysis

In statistical analysis, commercial rootstocks were not considered. Graphic were constructed on R with ggplot2 and ggdist packages. Correlation between traits were explored with Pearson correlation test. The PCA were performed according the year of field plantation for the $\delta^{13}C$ and the pruning weight. Commercial rootstocks (Börner, 110R, SO4, and 5BB) positions were indicated in individuals plots but they were not included in the PCA calculation. Missing data were imputed by the corresponding trait mean.

Best Linear Unbiased Predictors (BLUPs) were estimated for each trait in order to obtain the phenotypic values corrected for environment variability using the genotype replicates, the year of planting, and both year of experiment. The model for which the residuals information fitted the best and for which no collinearity between co-variables was low (VIF criteria) was selected.

$$P_{ghi} = \mu + G_g + Y_h + F_i + \varepsilon_{ghi} \quad (2)$$

Where P_{ghi} was the phenotypic value considering the genotype (G_g), the year of measure (Y_h) and the year of field planting of the plant (F_i). ε_{ghi} was the residuals variance. The genotype was considered as random effect in the model in order to obtain a variance-covariance matrix to calculate broad sense heritability (H^2). All the others factors were considered as fixed effects in the model. Because the pruning weight trait followed an exponential-like distribution, the square roots of phenotypic values were used and allowed to fit the model better.

The broad sense heritability of traits was calculated following equation 3,

$$H^2 = \frac{\sigma_g^2}{\sigma_g^2 + (\sigma_e^2/nrep)} \quad (3)$$

Where H^2 was the broad sense heritability of the trait, σ_g^2 was the variance explained by the genotype effect and $\sigma_e^2/nrep$ was the residuals variance extracted from the model divided by the mean number of repetition per genotype in the population.

These models were computed on R with the lmer package.

Correlations between the scion phenotype and root-related traits measured at a juvenile stage (obtained in Blois et al., submitted) have been explored. The BLUE values obtained for each traits have been used to calculate the Pearson correlation between traits genetic values.

GWAS

In order to access to the estimated genetic value of genotypes for $\delta^{13}C$ and pruning weight and to avoid the variance shrinkage from predictive models, the Best Linear Unbiased Estimate (BLUE) was calculated with a model similar to equation 1 but considering all the factors as fixed effects in a generalized linear model. The intercept of each genotype was then used as new phenotypic value in the GWAS. According to this procedure, we used only one phenotypic value per genotype for the two years of experiment and the two years of planting.

To carry out GWAS, the BLINK model was used on GAPIT3 (Wang and Zhang 2021) with default settings, implementation by major allele and MAF > 0.05 filtration. As a result, 87,589 SNPs were retained for further analysis. Population structure was considered as covariate with K=2 (Blois et al. submitted). The kinship was derived from pseudo-QTNs information directly from BLINK. We used a Bonferroni correction for significance thresholds, which were set at $0.05/n$ and $0.01/n$, being “n” the number of markers used. The variance explained by significant SNPs were estimated with BLINK results on GAPIT with a mixed linear model.

The genes linked to significant markers were obtained using the *V. berlandieri* annotated genome with a window corresponding to the LD extend (physical distance reached for $r^2=0.2$ according to Hill and Weir, (1988)) on the corresponding chromosome (average linkage disequilibrium decay was 2.2Kb as described in Blois et al. (submitted)). By this procedure the linked genes of all significant markers were obtained. Gene functions were defined according to information available on UniProt (The UniProt Consortium 2021).

5.3 Results

Rootstocks effect on the scion phenotype variability

At the phenotypic level, variability have been observed for both traits the pruning weight and the $\delta^{13}\text{C}$. The coeficient of variation of pruning weight varied from 0.46 when measured in 2021 for Experiment1 to 0.96 for the same plot measured in 2020 (Table 5.1). Concerning $\delta^{13}\text{C}$ which is calculated relatively to a standard, because the coeficient of variation is expressed as the pourcentage of the ratio between the standard deviation and the avarage of the trait, it was not possible to calculate this indicator for $\delta^{13}\text{C}$ (Oliver Brendel 2014). However we observed a standard deviation for $\delta^{13}\text{C}$ measured in 2020 from 0.82 for Experiment1 to 1.34 when measured in 2021 on the same plot (Table 5.1). The heritability (H^2) calculated with (3) revealed a moderate H^2 of 0.29 for $\delta^{13}\text{C}$ and a high H^2 (0.68) for the pruning weight after square root modification of the trait values.

Table 5.1 : Statistical results of traits conferred by the *V. berlandieri* rootstocks to the scion

Measurement	Trait	P1					P2				
		Min	Max	Av	StDev	CV	Min	Max	Av	StDev	CV
2020	$\delta^{13}\text{C}$ (‰)	-30.25	-22.16	-25.89	1.34	--	-	-	-	-	-
2020	Pruning weight (g)	0.10	75.80	14.34	13.75	0.96	-	-	-	-	-
2021	$\delta^{13}\text{C}$ (‰)	-31.54	-26.79	-29.15	0.82	-	-32.14	-24.72	-28.78	1.18	-
2021	Pruning weight (g)	0.00	150.00	63.54	29.19	0.46	0.00	145.00	29.75	21.10	0.71

The distribution of pruning weight values did not follow a normal distribution, however $\delta^{13}\text{C}$ values did (Figure 5.1). The pruning weight of Experiment1 increased in 2021 with plant aging (average = 63.54g) compared to 2020 (average = 14.34g). During the first year of growing, the Experiment2 have shown higher average pruning weight compared to Experiment1.

Considering the first year of development and growth of Experiment1 and Experiment2, the correlations observed between the pruning weight and $\delta^{13}\text{C}$ (Figure 5.2) were low ($r = 0.2$ for both). The second year of growing of Experiment2 revealed an increased correlation between the pruning weight and $\delta^{13}\text{C}$ ($r = 0.3$).

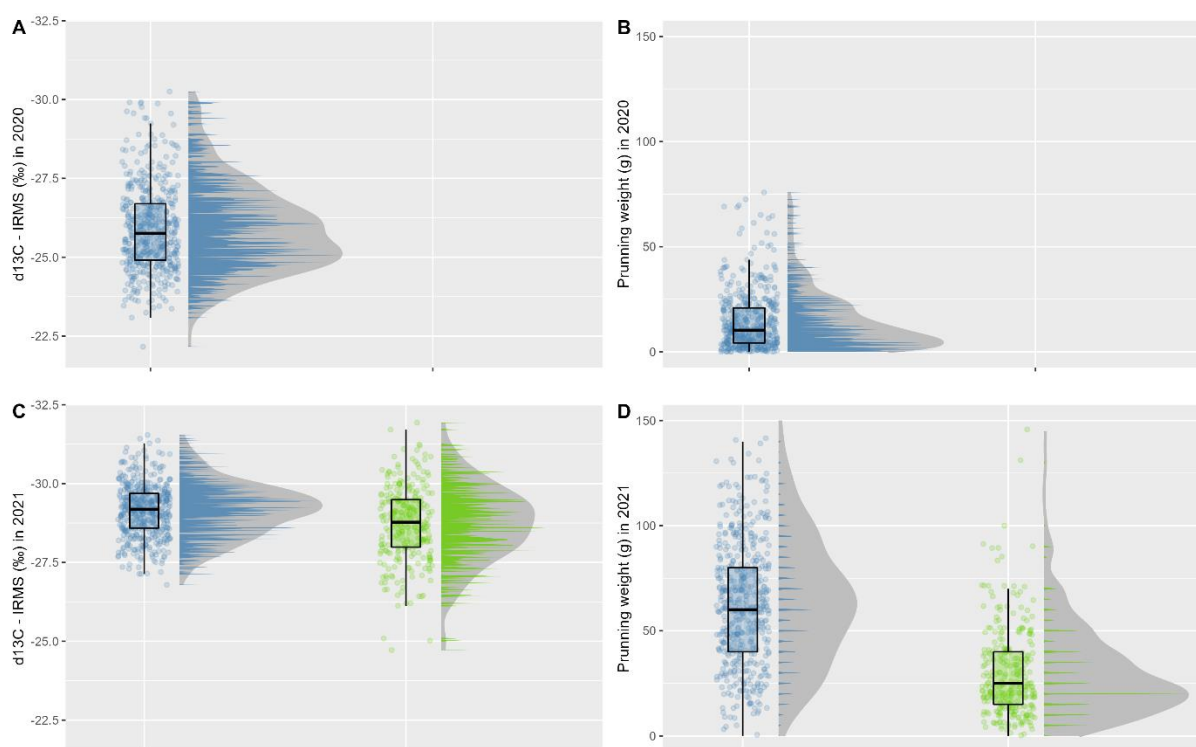


Figure 5.1 : Boxplots and distributions of traits conferred to the scion measured in Experiment1 (blue) and Experiment2 (green). For each trait, a boxplot is shown on the left and a bar plot distribution on the right with a density curve indicated in grey. The density curve was calculated with the `stat_lab` function of the `ggdist` package on R with an adjustment of 0.01.

Traits are the $\delta^{13}\text{C}$ measured in 2020 (A), the pruning weight measured in 2020 (B), the $\delta^{13}\text{C}$ measured in 2021 (C), and the pruning weight measured in 2020 (D).

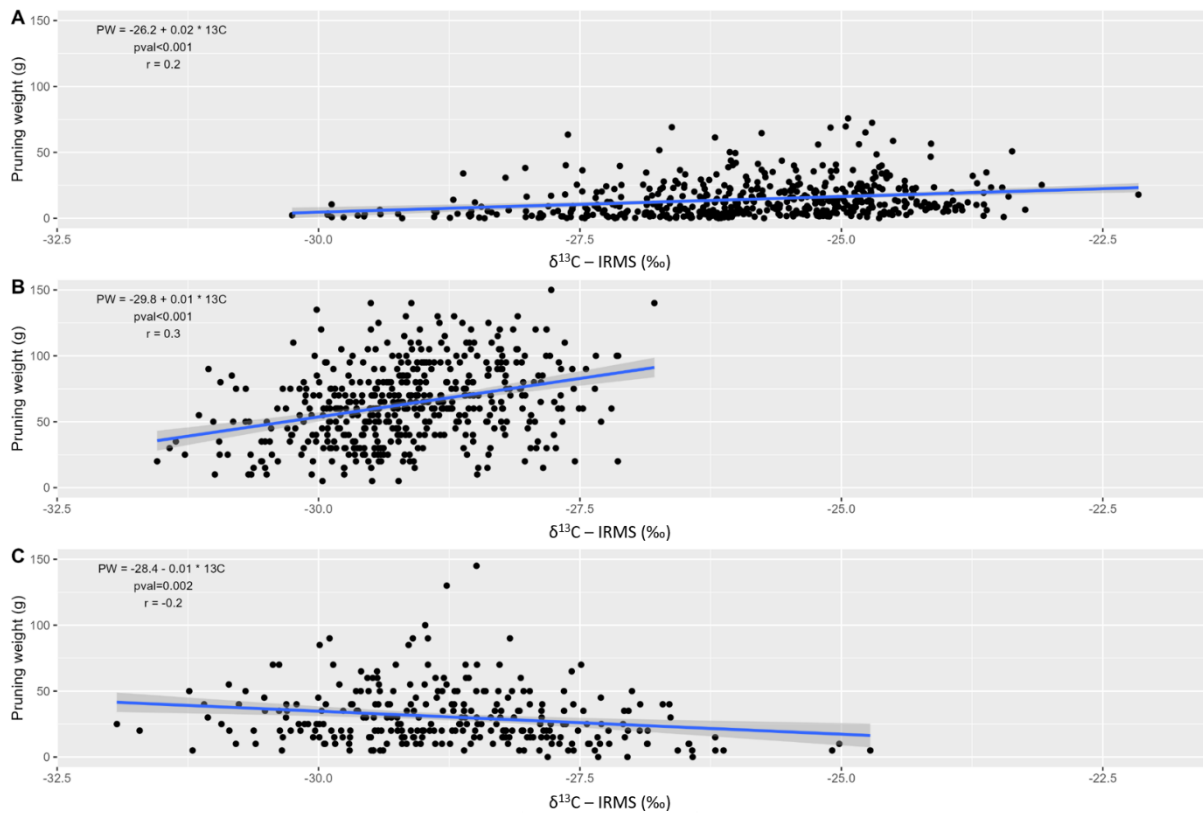


Figure 5.2 : Linear regression of the pruning weight and the $\delta^{13}\text{C}$ measured in 2020 (A) and in 2021 for the Experiment1 (B) and the Experiment2 (C). The equation of regression is indicated on the top left, the p-value being the significance of the impact of $\delta^{13}\text{C}$ on the pruning weight and "r" is the determining factor of correlation calculated with the Pearson method.

PCA were constructed for all traits separately for Experiment1 and Experiment2. For Experiment1, the two first dimensions allowed us to get 62% (Figure 5.3A) of the variability and because there was only two variables for Experiment2, 100% of the variability was observed (Figure 5.3B). On the individual graph of Experiment1 (Figure 5.4A) and Experiment2 (Figure 5.4B), commercial rootstocks (Börner, SO4, 110R, and 5BB for Experiment2) were grouped together.

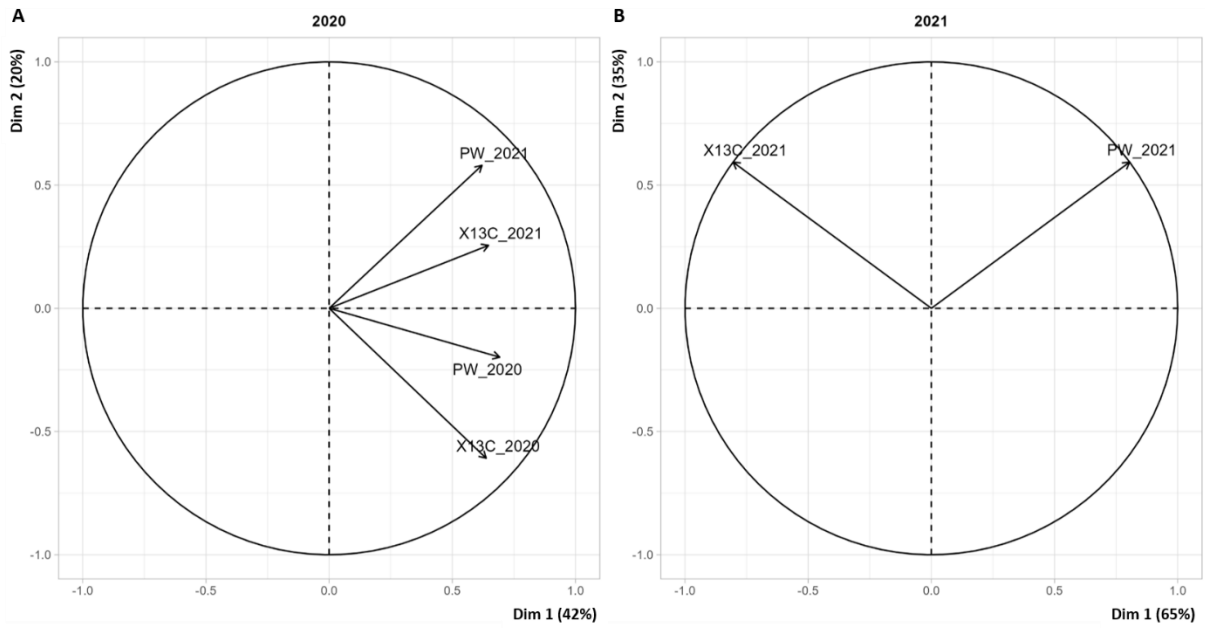


Figure 5.3 : Variables graph obtained from the PCA analysis for Experiment1 (A) and Experiment2 (B). Commercial rootstocks performances were not considered for the coordinates calculation.

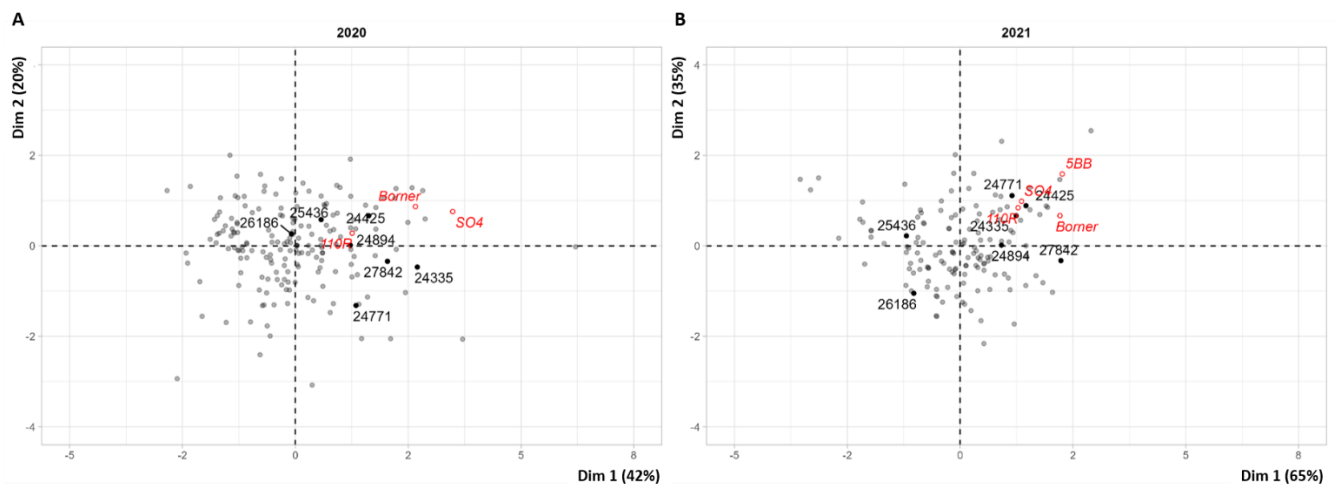


Figure 5.4 : Individuals graph obtained from the PCA analysis for Experiment1 (A) and Experiment2 (B). Commercial rootstocks (110R, Börner, 5BB and SO4) are indicated in red as supplemental individuals. Four *V. berlandieri* genotypes showing coordinates close to commercial rootstocks ones for the the two plots have been labelled (24335, 27842, 24425, and 24771). Additionally, promising genotypes highlighted for their root-related traits performances in Blois et al. (submitted) have been labelled as well (24894, 25436, and 26186).

GWAS for pruning weight and $\delta^{13}\text{C}$

The BLUE values of traits have been used to carry out GWAS. We were unable to detect any significant marker associated with the pruning weight but two significant markers have been highlighted as being associated with $\delta^{13}\text{C}$ (S2_17004748 and S17_6465816, Figure 5.5). The marker S2_17004748 explained 21.9% of the variability of the trait (Table 5.2) and was linked with the gene Vitvi02g00466 with a predicted function of tranmemembrane transporter activity for protein detoxification (The UniProt Consortium 2021). The marker S17_6465816 explained 23.3% of the variability of the trait (Table 5.2) and was linked to the gene Vitvi17g00537 probably coding for isopiperitenol/carveol dehydrogenase, mitochondrial-like (The UniProt Consortium 2021).

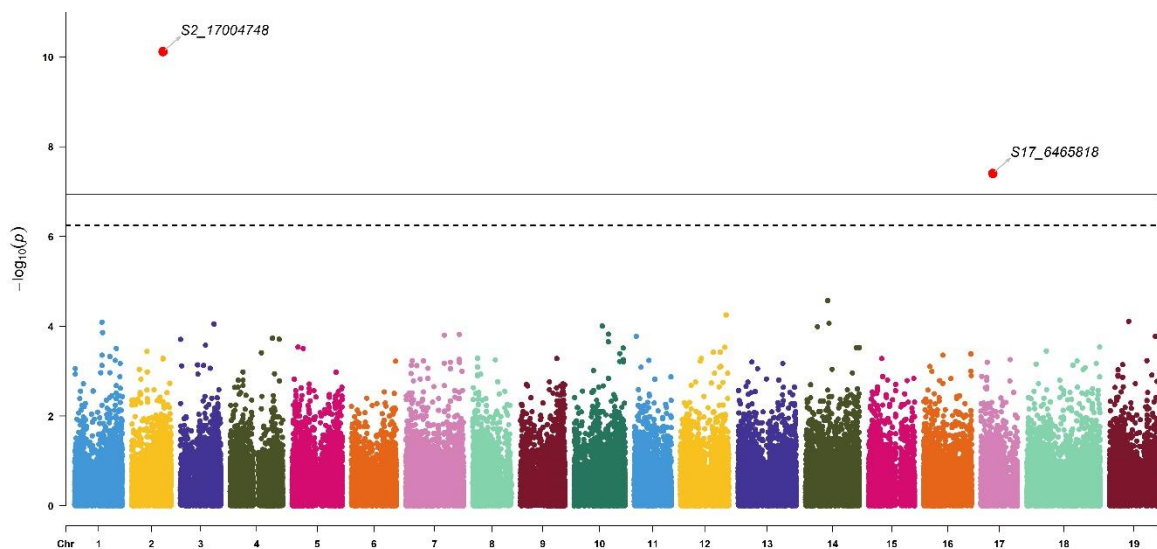


Figure 5.5 : Manhattan plot for SNPs associations with $\delta^{13}\text{C}$. The thresholds were calculated with the Bonferroni method for $\alpha = 0.05$ (dotted line) and 0.01 (full line). Significant signals have been highlighted in large red points for $\alpha = 0.01$. The corresponding QQ plot is presented Figure S 5.2.

Table 5.2 : Markers associated with $\delta^{13}\text{C}$ in the GWAS. The “ r^2 ” was the phenotypic variance explained by the marker, MAF is the minor allele frequency, and gene functions have been suggested on Uniprot.

Chr	Position	Trait	Effect	r^2 (%)	MAF	P-value	Size (bp)	Gene	Function	Source
2	17004748	$\delta^{13}\text{C}$	0.53	21.9	0.10	7.61E-11	5000	Vitvi02g00466	transmembrane transporter activity for protein detoxification	Uniprot
17	6465818	$\delta^{13}\text{C}$	-0.57	23.3	0.06	3.94E-08	2400	Vitvi17g00537	isopiperitenol/carveol dehydrogenase, mitochondrial-like	Uniprot

Wild rootstocks performances compared to commercial ones

On the individual PCA graph for Experiment1 and Experiment2 (Figure 5.4A and Figure 5.4B respectively) commercial rootstock were grouped together. Few genotypes have shown similar coordinates as commercial rootstocks ones for Experiment1 and Experiment2 (24335, 27842, 24425, and 24771). During the first year of growing for Experiment1 and Experiment2 commercial rootstocks were highly performant for the pruning weight and $\delta^{13}\text{C}$ (Figure S 5.1). However, during the second year of growing in Experiment2, commercial rootstocks were medium in term of traits performances (middle of the distribution).

Correlations with root traits

The genetic values of scion phenotypes obtained from BLUE have been correlated with the genetic values of root-related traits (Figure 5.6) obtained at a juvenile stage (one year after grafting) in Blois et al. (submitted). The pruning weight was positively correlated with the root dry weight (p-value = $1.4e^{-03}$), the number of large roots (diameter > 2mm, p-value = $5.6e^{-04}$) and the total diameter of the root system (p-value = $1.7e^{-03}$) which was the sum of primary roots diameter measured 4cm after the collar. The $\delta^{13}\text{C}$ was negatively correlated with the average diameter of roots (p-value = $3.5e^{-04}$) and the proportion of large roots (p-value = $8.1e^{-03}$).

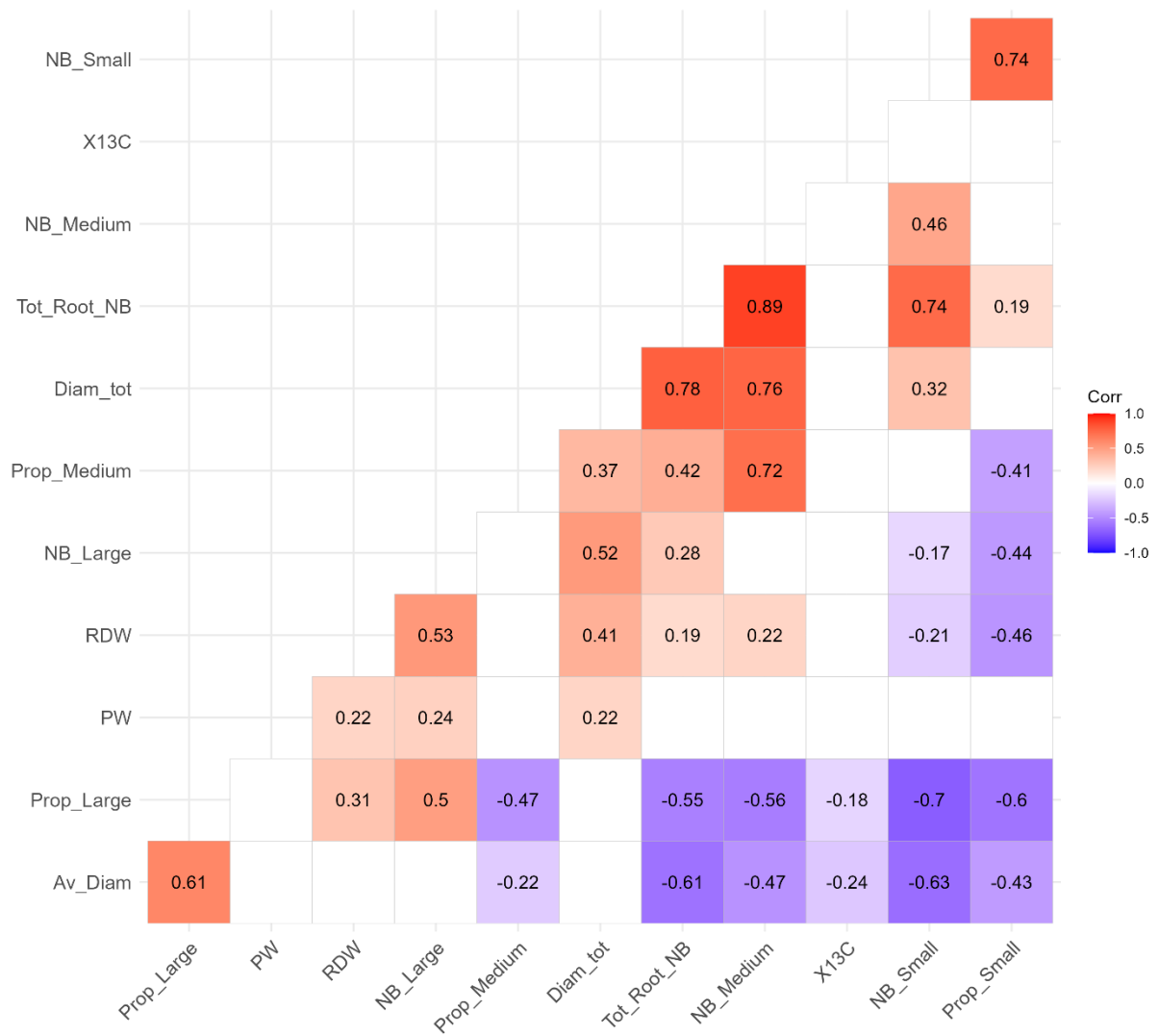


Figure 5.6 : Correlation matrix of genetic value of scion phenotype (PW= pruning weight and $\delta^{13}\text{C}$) and root-related traits obtained from Blois et al. (submitted), including the total number of roots (Tot_Root_NB), the average root diameter (Av_Diam), the total root diameter (Diam_Tot), the root dry weight (RDW), the number of small roots (1mm > diameter, NB_Large), medium (1 mm > diameter < 2 mm, NB_Medium), and large (2 mm < diameter, NB_Large) as well as the proportion of each class of roots (Prop_Small, Prop_Medium, and Prop_Large respectively). Pearson correlation have been used, and only significant correlation have been labelled (p -value < 0.05).

5.4 Discussion

In a grafted context, the wild population of *V. berlandieri*, a widely used species for rootstocks breeding (Galet 1988), have led to phenotypic variability in scion trait for pruning weight and $\delta^{13}\text{C}$. A GWAS carried out on these traits after the calculation of genetic values revealed two marker for $\delta^{13}\text{C}$ on chromosomes 2 and 17 explaining 21.9% and 23.3% of the trait variability, but we were not able to highlight marker associated with the pruning weight of the plants. When the traits values of the *V. berlandieri* population have been compared with commercial rootstocks (Börner, SO4, 110R, and 5BB), few genotypes have shown higher or similar values as commercial rootstocks. These genotypes could be considered in grapevine rootstocks breeding for their impact on scion genotypes.

Rootstocks effect on the scion phenotype variability

The role of root system in plant anchorage, water and nutrients uptake impact the vegetative growth of the upper part of the plant. The impact of root system variability for root-related traits on the vegetative growth have been observed previously (Montpetit and Coulman 1991; Colombi and Walter 2017; Yinglong et al. 2020).

In this study, the pruning weight was a proxy of plant vigor and have shown a high H^2 (0.68). The $\delta^{13}\text{C}$ is considered as an indicator of water use efficiency in plants (Farquhar and Richards 1984) because of the relation between the variability of this trait and water deficit events (Brüggemann et al. 2011). The measurement of this traits allowed us to compare species for their water use efficiency variability (Cernusak et al., 2007). In grapevine, the variability that exists between cultivars has been explored previously, revealing association with grapes water status (Gaudillere, Van Leeuwen, and Ollat 2002; Chaves et al. 2007; Bota et al. 2016). In our study carried out in the field, the plants did not experience water deficit during the two seasons, however, we were able to observe variability in $\delta^{13}\text{C}$ on the scion part when comparing rootstocks genotypes. Despite the absence of water deficit events, the $\delta^{13}\text{C}$ remains a good indicator of plant water use efficiency as suggested by Elazab et al. (2012). They studied four recombinant inbred lines of durum wheat in well-watered and water deficit conditions. They have observed correlations between $\delta^{13}\text{C}$ and root and aerial biomass accumulation for the well-watered context but no clear pattern were observed in water stress

context. Moreover, a recent study of Plantevin et al. (2022) on grapevine berry juice, confirmed that $\delta^{13}\text{C}$ measured in well watered condition discriminate well water deficit responses between cultivars. Our results confirmed previous studies carried out with a similar context of one scion grafted with different rootstock genotypes (Marguerit et al. 2012; Mairata et al. 2022). In the context of climate change, these results have shown the interest of including $\delta^{13}\text{C}$ in rootstocks breeding program for grapevine adaptation. At the phenotypic level, we have observed a moderate H^2 for this trait (0.29) which was similar to the H^2 calculated for this trait in *Pinus pinaster* (from 0.23 to 0.41, Marguerit et al. 2014) and grapevine (from 0.33 to 0.65, Marguerit et al. 2012).

At the statistical level, the use of a BLUP model which included all measurement increased the statistical power of our analysis by increasing the number of genotypes included to 211 (183 and 142 separately). The number of repetition by genotype increased significantly as well from 2.5 to 6.2. The calculation of H^2 and estimates values from BLUE model were more reliable in this way. A special attention has to be paid for the pruning weight which have required a square root transformation to fit with the model. GWAS results were then based on calculation made on these values.

GWAS for pruning weight and $\delta^{13}\text{C}$

In order to carry out GWAS, we used the BLINK (Bayesian information and Linkage disequilibrium Iteratively Nested Keyway) model for its higher performances in the detection of significant markers (Huang et al. 2018).

In a previous study carried out on a grapevine progeny, QTL have been detected for aerial biomass in a grafted context (Marguerit 2010; Tandonnet et al. 2018). In our study we were unable to detect QTL for the vigor conferred by the rootstock to the scion. Despite the high H^2 and CV, the variability observed at the phenotypic level was not associated with the genetic variability of the population. This can be due to the polygenic control of this trait which have not allowed us to highlight specific genetic regions involved in the determinism of plant vigor.

Two significant marker have been highlighted for $\delta^{13}\text{C}$ in this study S2_17004748 and S17_6465816 explaining 21.9% and 23.3% of the phenotypic variability respectively when based on BLUE values. Into the genetic region of the maker S2_17004748, the gene Vitvi02g00466 was detected with a predicted function of transmembrane transporter activity

for protein detoxification (The UniProt Consortium 2021). The gene contains two Multi Antimicrobial Extrusion (MATE) family function domains based on SMART information (Letunic, Khedkar, and Bork 2021) as drug and sodium antiporters (Hvorup et al. 2003). The marker S17_6465816 was linked to the gene Vitvi17g00537 with a predicted function of isopiperitenol/carveol dehydrogenase, mitochondrial-like (The UniProt Consortium 2021). The gene sequence contains a Pfam domain (Letunic, Khedkar, and Bork 2021) associated with polyketide and fatty acid synthase (Bonnett et al. 2013). These compounds could be associated with the plant osmotic regulation in water deficit context (Gharibi et al. 2016; Hodaiei et al. 2018) and lipid metabolism which is affected by drought stress event as it has been observed in *A. thaliana* (Gigon et al. 2004) or oat (Sánchez-Martín et al. 2018).

In previous genetic studies carried out on grapevine for $\delta^{13}\text{C}$, Marguerit et al. (2012) have detected 4 QTL in a grafted progeny without collocalisation with our results. Flutre et al. (2022) studied a *Vitis* species population for various traits including $\delta^{13}\text{C}$. They have detected several QTL for the $\delta^{13}\text{C}$ including two on chromosome 17 on positions 4819081 and 5948879, collocalising with our results (position 6465816). Despite the finding of markers on the same genetic area, the low linkage disequilibrium decay of grapevine limits the transposition of our results with the results of Flutre et al. (2022).

Wild rootstocks performances compared to commercial ones

Commercial rootstocks selected have been widely used in vineyards for their agronomic performances (Galet 1988). In our study, they were used as controls of the *V. berlandieri* population performances. During the first year of growing, commercial rootstocks have shown higher pruning weight and a lower $\delta^{13}\text{C}$ compared with the *V. berlandieri* population. However, it has been shown that the rootstock effect on the scion is cumulative during the first years of growing. Costes, Salles, and Garcia (2001) studied the effect of apple tree rootstocks on vegetative growth and observed an increased growth of plants with higher growth the year before. These results were confirmed later (Costes and Garcia-Villanueva 2007). In our study, during the second year of experiment, commercial rootstocks were in the middle of the population performances for both traits. This experiment has to be continued in order to confirm the promising performances of the best *V. berlandieri* genotypes of the population next years. Additionally, when comparing genotypes coordinates in a PCA,

commercial rootstocks were grouped together and few genotypes were very close to them for both years of experiment and the two plots (24335, 27842, 24425, and 24771). These genotypes could represent good candidates for breeding as well.

Correlations with root traits

Correlations between root traits and vegetative phenotypes, including plant vigor, have been observed previously. Montpetit and Coulman (1991) have detected a correlation between the number of adventitious roots and spring vigor in red clover. Colombi and Walter (2017) were able to show a correlation between the number of roots and shoot dry weight in wheat. Yinglong et al. (2020) compared the variability of 24 root-related traits and 4 shoot traits in wheat, highlighting correlations between root dry weight at different depths and shoot dry biomass and tiller number. These correlations have shown the interest of selecting genotypes for root-related traits in order to adapt crops species. In 2012, Wasson et al. proposed a breeding strategy for wheat in order to select plant for root-related traits such as root depth and radial hydraulic conductivity to increase the water deficit tolerance of the plant. In grafted plants, it is much easier to select plants for root-related traits because rootstocks are independent genotypes from the scion. In our study, the rootstock genotypes impacted the scion phenotypes for pruning weight and $\delta^{13}\text{C}$. In order to limit the impact of environmental variations from separated experiments for root-related traits and scion phenotyping, we used the genetic values of traits to figure out correlations. The root dry weight, the number of large roots and the total root diameter were correlated together and were positively correlated with the pruning weight. These root-related traits are linked to the overall root system biomass and their association with the pruning weight should be linked with the root:shoot ratio (Webster, 1995). The $\delta^{13}\text{C}$ was negatively correlated with the average root diameter and the proportion of large roots which were correlated together as well. The root diameter have shown to be associated with the hydraulic pressure of the root system, thick roots have a reduced hydraulic pressure and are more responsible of water transport than soil water extraction (Rieger et Litvin, 1999; Oliveras et al. 2003; Wang et al., 2016). However, plants have not faced water limitation during the growing period which have probably limited the impact of the root system in soil water extraction.

In a previous study made for root-related traits in the same population (Blois et al., submitted), 24335, 27842, 24425, and 24771 and genotypes were not identified as similar to commercial

rootstocks for their root performances. In a PCA constructed with root-related traits variations, these genotypes have shown intermediate coordinates traducing average values for most of root-related traits. In the same study, three genotypes were identified (24894, 25436, and 26186) for their root-related traits performances. In this study the genoytpe 24894 have shown similar performances as commercial rootstocks but the two others were not remarkable. Despite the interest of this genotype for breeding, other traits have to be measured in order to get more information of this genotype behavior in different climatic scenario.

Considering the aim of identifying root system ideotypes, it illustrates the difficulties in finding relevant root traits for plant improvement. Despite well known propositions as the steep, cheap, and deep ideotype (Lynch 2013), it shows the complexity of selecting a root system ideotype to adapt perenial crops. Moreover, the plant material used in this study was two and three years old which correspond to a juvenile stage. We expect variations in the root system development during next years of growing resulting in potential variations in the correlations at a mature state.

5.5 Conclusion

In our study, we have used the first wild population of grapevine rootstocks genotype. We have been able to observed phenotypic variability in conferred traits measured on the scion for the pruning weight and the $\delta^{13}\text{C}$. Two genetic marker have been highlighted in a GWAS fortheir association with $\delta^{13}\text{C}$ but no marker was associated with the pruning weight of the plants. These markers could be used in grapevine rootstock breeding as indicator of vigor and water use efficiency conferred to the scion. Moreover, the commercial rootstocks included in the experiment allowed us to compare the *V. berlandieri* population genotypes with performant and widely used rootstocks. As a result, four genotypes were detected for the performances very similar to commercial roostocks. One genotype identified in a previous study for root-related traits performances have shown good performances for scion conferred traits as well. These genotypes could be used in crossing of grapevine rootstock breeding programs.

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5.8 Supplemental data

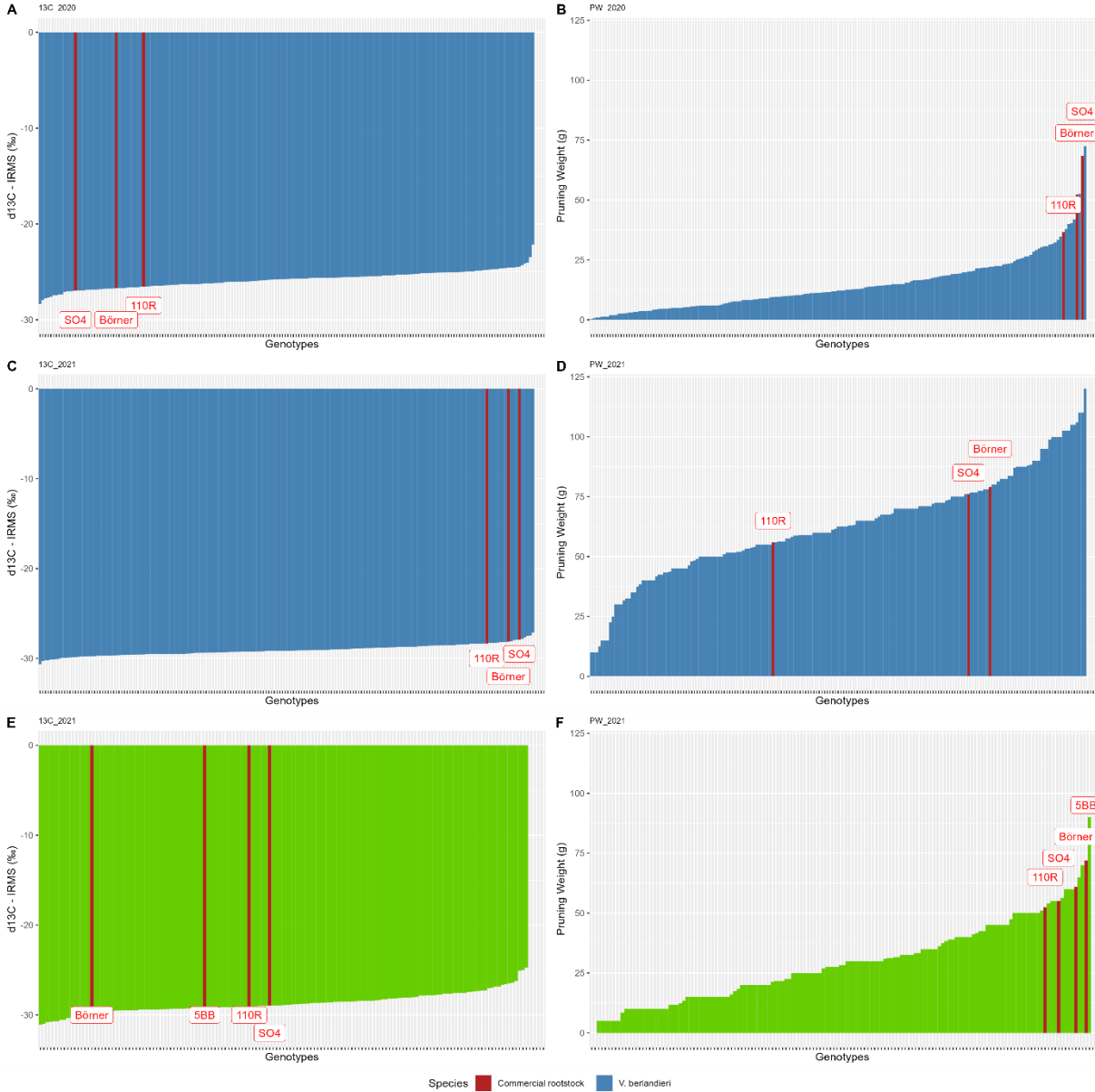


Figure S 5.1 : Distribution of $\delta^{13}C$ for the Experiment1 measured in 2020 (A) and 2021 (C), pruning weight measured in 2020 (B) and 2021 (D) for the Experiment1, the $\delta^{13}C$ measured in 2021 for the Experiment2 (E), and the pruning wieght measured in 2021 for the Experiment2 (F). Commercial rootstocks (Börner, 110R, SO4, and 5BB) position are indictaed with red lines.

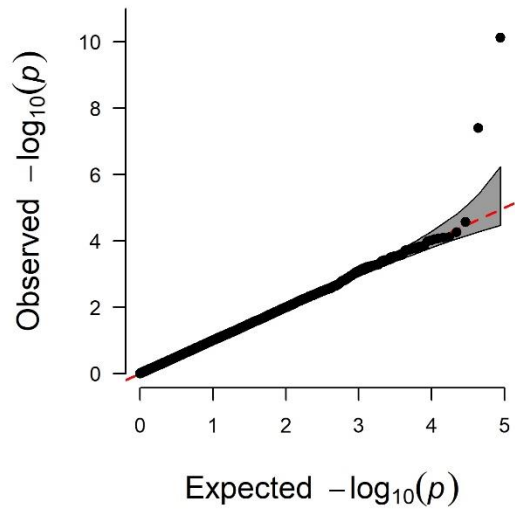


Figure S 5.2 : QQ plot, indicating the distribution of theoretical p-values and the distribution of observed p-value in the genome wide association study for $\delta^{13}\text{C}$.

Conclusion

In this chapter, we have observed variability and a medium to high heritability for traits conferred by the rootstock to the scion. Despite the lack of markers associated with the pruning weight of the plants, we were able to detect two markers associated with $\delta^{13}\text{C}$. Moreover, we have highlighted correlations between root-related traits and traits conferred to the scion. This study is at the front head of grapevine rootstock breeding because it is the first one carried out in field with a grafted grapevine rootstock mono species. Moreover, in this context, it is the first GWAS carried out at the genetic level for traits conferred to the scion. The markers and genotypes highlighted in our results are of major interest in grapevine rootstocks breeding, markers for $\delta^{13}\text{C}$ could be used to select genotypes conferring higher water use efficiency to the entire plant and the genotypes could be used in crossings in order to obtain new hybrids rootstocks which could increase the rootstocks diversity in vineyards.

Chapter 6: General discussion

“The best feeling in the world is the sense of mystery. Anyone who has never experienced this emotion, his eyes are closed.”

Albert Einstein

The aim of this chapter is to discuss our overall results. We have used a wild population of American grapevine rootstocks obtained after ampelographic exploration of the endemic region of *V. berlandieri* (Schmid, Manty, and Cousins 2009), a well-known species used in grapevine rootstock breeding (Galet 1988). The population of *V. berlandieri* preserved in Geisenheim, Germany, and the subset used in this project represent a unique gene pool to understand the genetic architecture of grapevine phenotype variability at the rootstock and the scion levels. In the context of climate change, we have selected traits for grapevine adaptation as root-related traits which are rootstocks own traits as well as pruning weight and $\delta^{13}\text{C}$ which are conferred traits. Using GWAS, we have detected markers associated with root-related traits and $\delta^{13}\text{C}$. Moreover, comparing *V. berlandieri* genotypes performances with commercial rootstocks ones, we are going to be able to select the most promising genotypes which could be used in grapevine rootstocks breeding programs.

6.1 Population sampling

6.1.1 Geisenheim population

The population sampling has been based on ampelographic criteria and the area explored was limited to 40,000 km² (Schmid, Manty, and Cousins 2009). However, it has been mentioned that *V. berlandieri* can be found in a larger area (Viala 1888; Rives 1974). Thus, it is reliable that the overall genetic diversity of the *V. berlandieri* genetic background is not completely represented in our sample. Despite the small geographic area explored, we have been able to find out two subpopulations with a genetic structure analysis. It is reliable to expect a higher genetic diversity in a larger area. When Rives (1974) went through Texas in order to collect *V. berlandieri* genotypes, he mentioned the *V. berlandieri* intra-species natural variation and paid a special attention in sampling genotypes geographically distant in order to increase the genetic diversity of his sampling. Moreover, the endemic region of *V. berlandieri* remains small compared to other American *Vitis* genetic backgrounds (*V. riparia*, *V. rupestris*, *V. cinerea*) (Péros et al. 2021). Because nearly all grapevine rootstocks hybrids have been obtained from these species, it could be of major interest to constitute gene pool collections for each genetic background in order to harness the genetic diversity available in natural conditions. This would allow us to understand the genetic architecture of various traits such as biotic and abiotic

tolerance, grafting success, root system architecture, and traits conferred to the scion which are of major interest in the context of climate change to adapt grapevine.

Considering the genetic diversity observed in the *V. berlandieri* gene pool, it could be interesting to include *V. berlandieri* genotypes of European collections in a larger genetic study in order to know to which subpopulation belong the parents used to create commercial hybrids rootstocks. It could allow us to evaluate the rootstock genetic diversity currently covered in vineyards. In another scenario, we could find out genotypes used as parents of commercial rootstocks as *V. berlandieri* cv. Resseguier 2 (female parent of 1103P, 225 Ru, 775P, SO4) or *V. berlandieri* cv. Boutin B (female parent of 110R, 140Ru) which do not belong to any subpopulation, highlighting a part of the *V. berlandieri* genetic diversity not covered by our sampling in Texas.

6.1.2 Population subset

The subset of the population initially included 286 *V. berlandieri* genotypes with the aim to represent the genetic diversity obtained from the sampling of the 78 female plants made in Texas, USA, and to use the best material available in term of vigor in order to obtain a sufficient quantity of vegetative material for grafting.

The grafting success of the two years of grafting led to a final population of 211 genotypes over the 286. The difficulties of grafting *V. berlandieri* is known and had led to limitations in using this genetic background in first hybrid rootstocks created to solve the phylloxera crisis (Galet 1988). This reduced the genetic diversity explored and led to different number of repetitions by genotype. Moreover, the number of genotypes coming from the same female plant varied leading to a kinship structure in the population because these genotypes could be full or half sibs. This structure has been considered in our GWAS analysis and gave us the opportunity to explore different statistical models.

The number of individuals was high in the experiment and led to robust and consistent statistical analysis and results. Unfortunately, few genotypes were not represented over the two years of experiment which unbalanced the gene pools composition when comparing the two years. In order to overcome this issue, it could have been possible to include only common

genotypes over the two years of experiment. However, 112 genotypes were common for the two experiments, which largely reduces the number of genotypes but increases the average number of repetitions per genotype. Population size has a strong effect on the power and the precision of fine mapping and Cockram and Mackay (2018) explained that increasing the number of genotypes is more suitable than increasing the number of replicates in QTL studies in order to promote the number of recombination events in the population. The same assumption can be done in association mapping. In our experiment, because all the shoot material available has been used for grafting, we have obtained the largest population as possible and excluding genotypes should not be advantageous. Moreover, the German team has sampled a larger *V. berlandieri* population (around 700 genotypes), they will use GBS data in order to find out correlation between genetic and phenotypic data. They have measured phylloxera responses and ampelographic traits. They have also planned to combine their GBS data with the GBS data presented in this document in order to obtain a larger data set.

6.2 Advantages and limits of the experimental design

In our study, Riesling have been used as the scion of all the population because of the plant material availability at the moment of the experiment in Geisenheim. However, it is known that the scion can impact the rootstock phenotype (Tandonnet et al. 2010) and some grafting combinations does not work in nurseries (Galet 1988). Thus, the markers detected in our analysis could be scion-dependant. A new experiment could be carried out with some others scions in order to check if the most performing rootstocks genotypes have the same behaviors with other scions.

Because of the volume limitation of root growing in pots and the complexity of reproducing natural conditions in greenhouses (Passioura 2006), our experiment have been made in field. The root phenotyping made before planting allowed us to get information about juvenile root-related traits and figure out correlations with the later phenotype in field. Because of the duration of a PhD project, we were limited to the two first years of growing in field which still correspond to a juvenile state. A third year of measurement will be added to the data set to compile three years of experiment at a juvenile stage.

It could be interesting to conserve the field for 10 years and restart at least the same measurement at 7 years old which correspond to a mature stage (Champagnol 1984) during at least two consecutive years. It could allow to: i) get a robust data set including several years of measurement; ii) observe the behavior of genotypes in different climatic scenario in the same region; iii) compare the juvenile phenotypes at the root and vegetative levels with the mature phenotypes.

Later on, the field could be removed and a new root phenotyping could be carried out. This would allow to measure the mature root system phenotype and find out correlation with the juvenile phenotyping. Figuring out correlation between the juvenile and the mature phenotype would allow to select juvenile traits of interest and then to reduce the time needed in breeding which is very long in perennials and represent important financial benefit for breeders (Luby and Shaw 2001). In perennials, because of the generation time, the genome size, the space needed for growing, and the cost of phenotyping, the number of genotypes included in studies is limited. Nowadays, the cost of genotyping has been widely reduced. It is of major interest to improve phenotyping methods in order to combine the genetic and phenotyping information in order to highlight phenotypic traits and genetic markers which could be used both at a juvenile stage in order to reduce the generation time needed, the number of genotypes, and thus the surface necessary for field experiments.

6.3 Which criteria are relevant for root system ideotype selection?

Because of the time needed for root phenotyping, we have limited the root system description to root-related traits presented before. However, different root traits have been investigated previously in various studies revealing relevant traits at the architectural (root length density, ramification, root tips diameter...) and anatomical (cortex thickness, xylem vessels description, number of root hairs, living cells size...) levels. Recently, a survey has been done during the 11th symposium of the International Society of Root Research (Delory et al. 2022). In this survey, objectives and advances on root phenotyping are summarized. The limitations in root phenotyping are mentioned, as the time needed, the expensive equipment and the lack of methodologies and statistical analysis available. However, the “root community” is mobilized and new tools are developed and are available for free as RootPainter or RhizoVision, which

should go in the direction of standardization of root phenotyping. Obviously, the most studied species are monocotyledonous crops (maize, wheat, barley, and rice) and no perennial woody plant is mentioned. Unfortunately, major questions remain unanswered as which root traits have to be targeted in breeding or how to optimize the carbon cost of the root system.

The overall objective studying root systems is to find ideotypes to face climate change. However, because root system ideotypes depend largely of the plant considered, the soil properties, and the climatic scenario, this question remains unanswered. Ideotypes have been proposed mainly for annual plants as crops adapted to infertile soils (White et al. 2013), nitrogen acquisition in maize (Mi et al. 2010), resistance to root lodging in maize (Bruce et al. 2001), or the steep cheap and deep ideotype for crops (Lynch 2013). Some evidences are transposable to woody perennial, as the rooting density in depth, the fine roots lifespan, or root diameter. However, because the root system of woody perennials has a stronger anchorage and storage function and stays in soil for several years, the interest of reducing the carbon cost of the root system by increasing aerenchyma or reducing the number of cortical cells layers (Lynch et al. 2021) remains uncertain and it could lead to a weak root system with reduced anchorage properties. More largely, dicotyledonous root system particularities remain unexplored in term of plant adaptation. The role of the root secondary growth has been poorly studied despite evidences in their functional significance in root water and nutrient absorption, carbon storage and micro-organisms interactions (Strock and Lynch 2020).

The use of ideotype faces a limit when considering the plasticity of traits. Because a genotype has to be considered in its environment, it is important to consider the variability of a trait in different environments. The ability of a genotype to react to environmental variation is the plasticity (Bradshaw 1965; 2006), which can also be considered as a quantitative trait (Lacaze, Hayes, and Korol 2009).

In the context of climate change, there is a particular attention to pay in the balance between fixed advantageous traits, and the plasticity of traits in order to get the ability to adapt to various external stimulations. This has been discussed by Lynch (2018) who defined the input level (high or low) of agro systems as a criteria of choice in annual crops. It is suggested that low input agro systems have to focus more on plasticity than high input agro systems

(Schneider and Lynch 2020). Once again, because of the lifespan of perennials root systems, the chance to face environmental variations during their lifetime increases compare to annual crops. Thus the need of conserving plasticity in perennials breeding appears of major interest.

Moreover, the plants were planted in pots during the first year of growing. The pots volume led to limitations in the root system growth and development. Thus, the plants have not fully expressed their root growth potential and different results could would have been found if the pots volume was higher or if the plants were set up in the field. We expect strong variations in root system profiles due to the plant aging and to the substrate of growing (from the pots to the field) (Passioura 2006). In pots, water relations, soil aeration, microbial activity, and temperature differ widely from field conditions (Passioura 2006). The root system growth and development being closely related to these conditions, performing genotypes for their root-related traits in pots could be totally different after a few years of growing in field.

6.4 What about scion conferred traits?

In the same way as the gap between pot and field conditions, it is very complex to catch the environmental variability in the field. We have measured the pruning weight and the $\delta^{13}\text{C}$ on the scion part. Because scions were from the same clone of Riesling, we have considered the phenotypic variability as being due to the rootstocks genotypes. During the project, no water deficit has been experienced by the plants according to the values of pre-dawn water potential observed, thus we were not able to compare our results for $\delta^{13}\text{C}$ in well-watered and water deficit conditions. During the last year of experiment (2022), a low to medium water deficit has been experienced by the plants. Two samplings were done for $\delta^{13}\text{C}$ analysis before the water deficit event from (pre-dawn water deficit = -0.44 bars to -1.37 bars) and at the end of the water deficit (from -1.45 bars to -6.35 bars). The results will complete our data set and is going to be included in our modes to actualise the GWAS as well as the pruning weight that I going to be measured in April.

In our study, the variability and the heritability of traits measured on the scion part were promising to carry out GWAS. However, no marker has been highlighted for the pruning weight. Few explanations can be proposed for this, firstly the impact of external factors has been corrected in the BLUE model and has limited the markers detection; secondly it is known

that the rootstock impacts the scion phenotype in grafted plants (Webster 1995; Warschefsky et al. 2016; Ollat et al. 2017) but in the interactions between the scion and the rootstock, the rootstock is affected as well (Proietti et al. 2008; Tandonnet et al. 2010; Clingeleffer et al. 2019; Meneses et al. 2020). Thus, a part of the variability observed is expected to be due to the scion × rootstock interactions and not only to the rootstock. The third hypothesis concerns the involvement of various genetic regions in the determinism of this trait which could make it difficult to detect significant markers. The fourth could be due to the rapid linkage disequilibrium decay, then the genetic regions associated with the trait could not be covered by the markers set.

Our results represent the first insights on the scion responses variability when grafted with a rootstock mono-species natural population. Our results are sufficient to show how much the genetic diversity available in natural conditions could permit to adapt grapevine in different ways by controlling more precisely plant vigor or water use efficiency for example.

6.5 Genetic insights

6.5.1 *V. berlandieri* reference genome

To process GBS data, a reference genome was needed. Before the project, a long read sequencing has been carried out allowing to acquire the first high quality reference genome for *V. berlandieri* (presented in chapter 3). This reference genome will be used in next genetic studies carried out on the *V. berlandieri* species. Moreover, this genome will be included in a pangenome project in the EGFV team. A pangenome, based on *V. berlandieri*, *V. riparia*, and *V. rupestris* high quality long read sequencing, will be constructed. The aim of this project is to dissect the genomes of the three genetic backgrounds the most used in grapevine commercial rootstocks. Then each genome will be divided into three parts, the core genome which is shared between the three genetic backgrounds, the dispensable which is shared between two genetic backgrounds and the specific which can only be found into one genetic background. Then three commercial rootstocks will be sequenced with long reads technology: SO4 (*V. berlandieri* × *V. riparia*), 110R (*V. berlandieri* × *V. rupestris*) and 3309C (*V. riparia* × *V. rupestris*). These commercial rootstocks will be compared with the pangenome in order to test its consistency. The pangenome could be used later on for alignment in grapevine sequencing.

6.5.2 How much heritability is in GWAS?

In order to detect markers associated with a trait, GWAS are more powerful than progeny-based quantitative genetic studies because the genetic variability is not limited by the recombination events resulting from the crossing of two genotypes. However, two main problems arise, the first is the detection of false positive signals and the second concerns the statistical power limitation or the detection of false negative signals (Borevitz and Nordborg 2003).

The false positive signals detection which are markers statistically associated with a trait whereas they are not involved in the determinism of this trait. This can be due to the structure that exists in natural population in which subgroups contain genotypes with a higher level of genetic similarities compared to those present in the population. As an example, a rare allele in the population can be shared by all genotype of a subgroup leading to unbalanced dataset. In our case, we have considered the structure of the population and revealed two subgroups which have been considered in GWAS in order to control the false positive detections (Pritchard, Stephens, and Donnelly 2000). However, according to the method used, the number of subgroups suggested can vary as it was the case when using a clustering method based on Roger's genetic distance (Voss-Fels et al. 2015). According to the number of subgroups considered, different results can be obtained in GWAS. In our study, because of the small geographic area of the plant sampling we decided to limit the number of subpopulations as two (as suggested by STRUCTURE) and our choice has been supported with environmental evidences as altitude.

The second limit due to the false discovery rate can also be due to the population structure and to the statistical model used, multilocus models being considered as more performant (Borevitz and Nordborg 2003). In our case, the structure was already taken into account and we decided to use the most recent GWAS model BLINK which have shown very good performances when compared to other models (Huang et al. 2018). However, model comparison has been done rapidly and underexplored. Moreover, because we are studying correlated traits, it could have been interesting to test for multi-trait mixed model (MTMM, Korte et al. 2012) in order to consider the intra and inter traits variations. It would allow to

detect markers with pleiotropic effect on different traits. However, this kind of models have been compared to single trait models and did not outperform them for marker detection (Merrick et al. 2022).

6.5.3 The specific case of grapevine genetics

In grapevine, the linkage disequilibrium decrease rapidly requiring a high number of markers to capture the genetic variability of this species. In domesticated *Vitis vinifera*, several genetic regions have been selected leading to an increase of the linkage disequilibrium in these regions. The experiment of Migicovsky et al. (2017) illustrates this phenomenon for the grapevine sex locus. They have obtained a small number of markers and were not able to detect markers for various traits but they were able to detect the sex locus thanks to the increased linkage disequilibrium in this region. In natural population, this kind of “high linkage disequilibrium” regions can be due to natural selection for advantageous traits.

In our study, we were limited by the geographic area of sampling which have led to limitation in the genetic diversity observed. This could have led in turn in limitation in the variability of traits. However, the phenotypic and the genetic diversity in the population allowed us to carry out GWAS and detect markers associated with root-related traits as well as $\delta^{13}\text{C}$.

6.5.4 How to use associated markers

We have based our genetic analysis on genetic values of traits thanks to BLUE models, and we have controlled false positive and negative signals detection by using structure information and selecting the more accurate model available in order to highlight the more relevant markers.

Most of the time, the MAS opportunity is mentioned when markers are found in quantitative or association genetic studies. However, MAS applications have concerned mainly traits with a simpler genetic architecture such as disease and pest tolerance which are related with biotic factors. More complex traits, as abiotic factors tolerance, growth, and development are difficult to improve by using a few genetic markers because of the polygenic determinism of these traits. In these cases, MAS remains more complex to apply.

6.6 Perspectives

The aim of this last part is to suggest next steps, firstly for the project and secondly for the grapevine adaptation to water deficit events thanks to rootstocks breeding.

The project has started by the grafting of the population of *V. berlandieri*. Thus, it has been a good opportunity to observe root system development at a juvenile stage one year after grafting. Then, plants have been planted in field and a few traits were measured at the scion level. Moreover, all genotypes have been sequenced during the project. In order to reduce the time needed for perennial breeding, it could be of major interest to find out correlations between juvenile and mature traits. Because the root and scion phenotype initial conditions are known, this material should be conserved in order to continue its analysis. This field could be maintained until the vines reached 7 years old, which is a clear mature stage in vineyard (Champagnol 1984). During three years at mature stage, the same measurements ($\delta^{13}\text{C}$ and pruning weight) could be done to compare the juvenile and mature stages. At mature stage (2023 for Experiment1 and 2024 for Experiment2), we could measure the yield of genotypes because it is a trait of interest in vineyards. After this period, the field should be dug out in order to phenotype the root system and compare it with juvenile root systems. Then correlations between root and shoot traits at juvenile and mature stage could be explored once again.

Which root phenotyping for the end of the field?

A major point of discussion arises concerning the root system phenotyping. During our experiment, we have limited the root system phenotyping to simple traits because we had no idea about the variability of these traits in a natural mono-species population, cultivated in pot during one year after grafting. According to our results, it could be interesting to measure more traits at the root system level. Root systems could be phenotyped at the architectural or anatomical level. Root system architecture provides information on the volume of soil explored, the depth, and the density of roots at different depths. This is related with the soil resources reachable by the plant. The anatomical level is related with the root system hydraulic pressure and the carbon cost of root system growth. These traits have been

highlighted as criteria of root system ideotype in annual plants (Lynch et al. 2021) and should be investigated in perennials.

Because of the number of individuals in the field and the difficulties in phenotyping root systems, we have to select informative root-related traits. It is known that grapevine root systems grow deeply in the soil and the excavation process will probably damaged root systems leading to bias in phenotyping. Because we were not able to find relevant high-speed root phenotyping protocole in field, we would like to propose a semi-automated root phenotyping (Figure 6.1) thanks to image analysis detailed bellow.

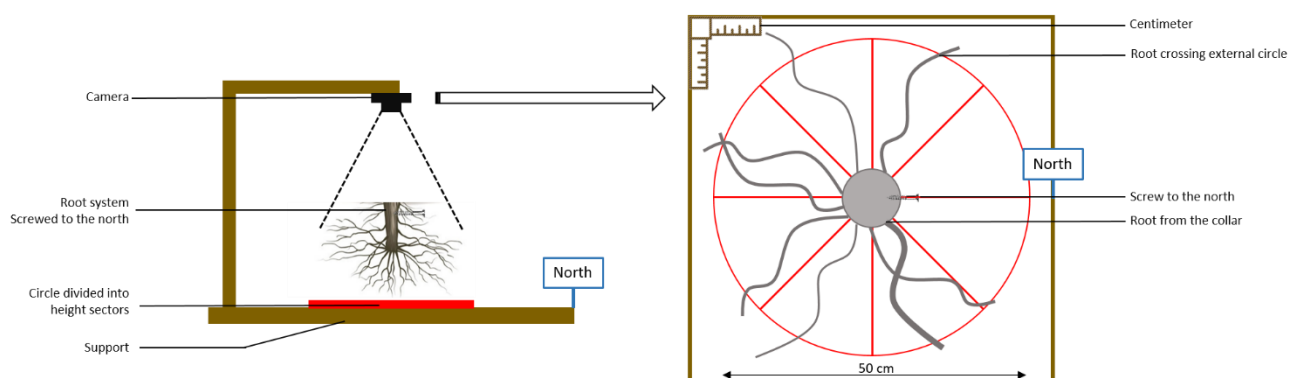


Figure 6.1 : Schematic root phenotyping set up. The right side show the material used and the left side shows the photo obtained from which root-related traits will be measured.

This experimental design proposed here results from personal communication with Clément Saint-Cast (2022) adapted from unpublished tree root systems high-speed phenotyping used on a sample of 1040 trees. The objective of this root phenotyping is to measure root traits at 25 cm from the collar and observe the root distribution around the plant, considering the plant position in the field. To do so, a screw will be screwed to the north face of each plant before digging out the plants. Then, plants have to be excavated, the vegetative part pruned, and the root system washed with pressurized water. Root systems will be placed in the middle of a circle (50 cm diameter) divided into height sectors drawn on a white painted wooden support. The screw will allow to localize the north face (rows are oriented north-south) of the plant. The photo obtained with the camera will be used in image analysis in order to measure various traits at 25 cm from the collar: root number, root number per sector, root average section, root total section, root section density per sector, volume of roots and maximum azimuth without rooting. Thank to the directional indication of each plant, we would be able to

compare the root distribution with plants position in the field. These traits would allow to observe the rooting patterns of each plants. We expect that the ability of genotypes to produce a large number of roots and spread them in all directions should be advantageous for mineral and water absorption. Then, the photo could be used for further visual traits evaluation. As an exemple, it could be possible to use similar scales to OIV disease evaluation (score from 1 to 9) for root branching and fine root density. This root phenotyping method could be done for one week in the field. Then, image analysis could be achieved after 2-3 months. Because genotypes are already available, all these traits could be used in GWAS later on.

During the project, Mathieu Larrey realized an intership and worked on grapevine root system growth and development. Three rootstocks were used (RGM, 110R, and 140Ru) and grown in tubes of 40 cm height and 14.5 cm of diameter. After 30 days, all plants reached the bottom of the tube. Thus, it was not possible to compare the genotypes for root depth but significant differences were observed for the root length density at different depth. RGM have shown higher root length density in first layers whereas 110R and 140Ru have shown higher root length density in depth. The tube experiment was adapted to observe the 3D architecture of root systems but less adapted for measuring the root system morphology than rhizotrons. Tubes and rhizotrons are suitable for observing root traits and it could represent a good supplemental experiment to get insights in the growth and development of root in depth. However, the number of genotypes considered in our study makes it complicated to use these methods.

What about multisite experiments?

At the genetic level, in order to encompasses the variability of traits due to environment, constructing the same experimental design in another region could improve the statistical accuracy of models and the reliability of results by considering the genome \times environment interactions. The genotypes used in our study remain available in Geisenheim which could allow to set up the same experiment in different locations. Doing so, we could check if genotypes ranks change in different environment, which is of major importance for breeding (Kang 2002).

In a communication from Anne Fennel during the XIII International Symposium of Grapevine Breeding, multisite experiment has increased the reliability of results in grapevine. The best genotypes detected in a population for a trait of interest can change according to the environmental interactions that occur in a specific environment. Thus, in order to be able to propose a few genotypes to include in grapevine rootstocks breeding programs, repeating the same experimental design in contrasted environments could be useful.

Because field experiments are complicated to set up for perennials, it could be possible to check for genotype \times environment interactions by selecting contrasted genotypes for root-related traits and for traits conferred to the scion. As an example, 30 contrasted genotypes could be selected and phenotyped in Geisenheim. According to the variation in genotypes ranks, a larger experiment could be considered in order to dissect deeper the genome \times environment interactions.

How to complete our results with new quantitative studies?

Because grapevine genetic studies are scarce in a grafted context, it is not possible to include our results in a meta-QTL analysis for our traits. However, to complete our results, a larger *V. berlandieri* population will be explored at the phenotypic and the genetic levels by the grapevine breeding institute of Geisenheim in the few next years. In France, a novel progeny *V. berlandieri* \times *V. rupestris* of 300 genotypes has been created and grafted with two scions (Cabernet-Sauvignon clone 169 and Riesling 24-209) and the genetic architecture of root-related traits will be explored. The same root phenotyping method as in our studies has been followed. Thanks to the parental genetic maps, we will be able to observe the recombination rate around the markers highlighted in our study as well as the allelic segregation of our markers within the progeny.

What monitoring for current diversity in V. berlandieri and other species?

This work has demonstrated the interest of exploring the genetic diversity of natural population of American rootstock species. The genetic material available in natural conditions has not been used yet in breeding program and could be a way of grapevine adaptation. However, it implies that other American *Vitis* genetic backgrounds (*V. rupestris*, *V. cinerea*, *V. riparia*) should be explored in order to select the best genotypes from each species. In this

case, SSR markers could be used in order to distinguish true genotypes of a species from natural hybrids from overlapping geographic distribution areas.

Our results about the structure of the *V. berlandieri* population could be used to explore the genetic diversity of parents of commercial hybrid rootstocks. According to the VIVC database, 56 *V. berlandieri* genotypes are available in germplasms. These genotypes could be included in a PCA based on genetic markers information to observe the distribution of these genotypes in subpopulations. Several scenarios are expected (without considering false identification of *V. berlandieri* in germplasms), i) nearly all genotypes come from a single subpopulation of our study highlighting either a bias in the sampling done by Viala and Rives during the collection done to solve the phylloxera crisis or the higher performances of one of the two subpopulation in vineyards; ii) the 56 genotypes are spread in the two subpopulation, indicating that the natural genetic diversity observed in our study is covered by the rootstocks available in germplasm; or iii) the genetic diversity of the 56 *V. berlandieri* is larger than the one observed in our sampling, showing that our sample do not cover the real diversity of the *V. berlandieri* genetic background. Knowing which is the right scenario could allow us to better contextualize our results.

Additionally, a new project will start in 2023 in which Marina de Miguel planed to explore the genetic diversity of American, European (*Sylvestris*), and Asian grapevine species. In total 12 species will be studied (50 genotypes, obtained from germplasm collection) in order to dissect the inter and intra species genetic diversity. The genetic structure of *V. berlandieri* has been widely discussed in this document, in the same frame as the Marina de Miguel's project, it would be interesting to use the genetic diversity available in germplasm around the world in order to characterize the genetic diversity used and usable in breeding. Here, we are not interest in phenotyping traits but only highlighting the genetic structure of individuals in germplasms. In the same frame as it has been done by Péros et al. (2011; 2015; 2021), we propose a collaborative project including the collections of American grapevine species from INRAE (Vassal and Bordeaux, France), the grapevine breeding institute of Geisenheim (Germany), FEM (San Michele, Italy), and USDA (Davis and Geneva, USA). Each partner could take in charge the sequencing of his own collection and share data for the project. The sequencing could be done by GBS method in order to obtain a fine SNP mapping. This fine

mapping is reachable now thanks to the international community efforts to obtain reference sequence of various American species such as *V. riparia* (Girrollet, Rubio, and Bert 2019), *V. amurensis* (Wang et al. 2021), *V. berlandieri* (Blois et al., submitted), and nexts are planned to be done in different project in Bordeaux and other labs. The first step would be to use the genetic diversity of each genetic background in order to highlight an “consensus genome” of each species. Then it will be possible determine the proportion of each “consensus genome” present in natural and domesticated hybrids. Then, we could improve the quality of grapevine genomes assembly and access information about structural and functional gene annotation (Murat et al. 2017). This information represents a highly valuable resource to understand the genetic architecture of traits of interest in breeding.

Chapter 7: Conclusion

*“Two roads diverged in a wood, and I, I took the one less travelled by, and that has made all
the difference”*

Robert Frost

Our work has highlighted two subpopulations in our *V. berlandieri* sampling. We were able to detect phenotypic variability for root-related traits in the population at a juvenile stage and genetic regions were associated with these traits. Variability has been observed for traits conferred to the scion and genetic regions were associated with these traits as well. Moreover, correlations have been observed between root-related and conferred traits. Few *V. berlandieri* genotypes have been identified for their root-related performances and their conferred performances when compared to commercial rootstocks.

Because water deficit responses are complex traits, we aimed to find out root-related traits correlated with water deficit responses. However, the correlations between root-related traits and $\delta^{13}\text{C}$ were light. The $\delta^{13}\text{C}$ measurements have been done in a no water deficit context, and we can expect different plants behaviors when experiencing water deficit. Thus, the incoming results for $\delta^{13}\text{C}$ measured in 2022 after water deficit could lead to variations in the correlations observed between root-related and conferred traits.

This work has opened a door on grapevine rootstocks genetic diversity, has been presented to the scientific community during an international communication, submitted as two papers to scientific journals (a third one will be submitted later), and strengthened the collaboration between scientists from Bordeaux and Geisenheim.

In the context of grapevine adaptation, our work provided insights in genetic resources available in natural conditions. We have demonstrated the interest of phenotyping root-related traits which have shown moderate to high heritability allowing us to detect significant genetic markers associated with these traits. Now, it is necessary to find out which root traits are associated with agronomic traits of interest. It reinforced the idea that the rootstock constitutes a strong way of adaptation that remains under-exploited. Moreover, studying natural genetic resources made it possible to compare the genetic diversity already used (commercial rootstocks) with the available one (population from natural conditions). This approach had never been used in grapevine.

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