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Grafting, the most sustainable way to control phylloxera over 150 years

Nathalie Ollat[1], Olivier Yobrégat[2], Thierry Lacombe[3], Markus Rienth[4], Sébastien Julliard[5], Maria Lafargue[1], Jean-Pascal Tandonnet[1], Jean-Pascal Goutouly[1], Sarah Jane Cookson[1], Marina de Miguel[1], Daciana Papura[6], Elisa Marguerit[1]

[1] EGFV, University of Bordeaux, Bordeaux Sciences Agro, INRAE, ISVV, 33882 Villenave-d'Ornon, France
[2] IFV, V'Innopôle Sud-Ouest, 81 310 Peyrole, France
[3] AGAP, Univ Montpellier, CIRAD, INRAE, Institut Agro, 34398 Montpellier cedex 5, France
[4] Haute école de Viticulture, Changins, CH-1260 Nyon, Switzerland
[5] Conservatoire du Vignoble Charentais, 12 route de l'ancien séminaire, Richemont, 16370 Val-de-Cognac, France
[6] SAVE, Bordeaux Sciences Agro, INRAE, ISVV, 33882 Villenave-d'Ornon, France

Abstract. Just over 150 years ago, grape phylloxera, *Daktulosphaera vitifoliae*, was introduced to Europe from North America via imports of plant material. This aphid-like insect has spread rapidly to most vineyards, causing rapid and lethal decline of *Vitis vinifera*. What happened in the second half of the 19th century in response to this pest has shaped the way in which grapevines are cultivated and wines produced in worldwide. Among the solutions identified, grafting onto rootstocks with American *Vitis* backgrounds gradually came to the fore for its many advantages. Compared with other methods of control, it was seen as a sustainable, feasible on large scale and economical for winegrowers. Grafting grapevine can be considered the first widespread biological control method in modern agriculture and offers many benefits for plant adaptation to the environment. This paper provides an overview from the history of the phylloxera crisis to the latest scientific findings on the control of phylloxera. It aims to remind us that grape phylloxera is not an issue of the past and that the utmost vigilance is still necessary. Despite some limits, grafting remains the most sustainable means of combating phylloxera and meeting the viticultural challenges of tomorrow.

1. Introduction

During the first half of the XIXth century, French viticulture was very dynamic with a lot of new plantations and innovations, especially in the South of the country. The use of new growing practices (fertilizers, animal traction etc.), the absence of major diseases, a high demand and the development of transportation means were the main factors explaining the sharp increase in vineyard areas in France (from 1.5 Mha in 1789 to 2.4 Mha in 1874). Vineyards were replacing annual and subsistence crops. This period is considered as the Golden Age of French viticulture [1]. The introduction of the fungus *Erysiphe necator* and the subsequent general epidemy of powdery mildew from 1851 was the first major setback in this Golden Age, despite the fact that the disease was quickly under control with the use of sulphur spraying. The first plant decay linked to phylloxera *(Daktulosphaera vitifoliae,* Fitch, Hemiptera: Phylloxeridae*)* were recorded in 1863 and the insect spread very quickly. In 20 years, 1 Mha were totally destroyed and 0.6 Mha infected [2]. It was not a simple disruption, but a catastrophe, which had enormous consequences of the grape growing sector and associated industries. The grape phylloxera outbreak generated a deep general economic crisis, especially in France where the total costs of the damages were estimated to be superior to the amount of money given to Germany as the debt of 1870 war [1]. The area of vineyards decreased to 1.7 Mha in 20 years with major consequences over several decades in terms of production, wine prices, development of fraudulent practices, unemployment, emigration and geography of vineyards. This crisis (along with other plant health crises from the second half of the XIXth century) and the ways they were solved modified totally growing practices and resulted in a major reorganization of the wine sector in France, with consequences all over the world. Meanwhile it was a period where agricultural practices in general evolved considerably with increasing scientific knowledge.

During the first half of the XIXth century, the exchanges with North America boosted the introduction of American *Vitis* species, initially as curiosities in botanical gardens such as the one from "Jardin du Luxembourg" in

Paris and in private collections throughout France [1, 3]. The introduction of powdery mildew in the middle of the XIXth century enhanced the importation of such species, which were shown to be *E. necator* resistant. Later it transpired that these species were both the cause and the most efficient solution to control the phylloxera plague. As suggested by L. Laliman (winegrower) during the Beaune congress in November 1869 [4], soon after phylloxera was identified,, the advantages of using American *Vitis* species were subjected to many controversial debates, which slowed down the replanting process. This remains an issue for own-rooted vineyards under the threat of phylloxera today.

Grafting is one of the most ancient horticultural techniques, originating several millennia ago in China or Mesopotamia. For grapevine, it was mentioned very early in religious textbooks and by the first agronomists to increase productivity or to change varieties without uprooting [5]. However, it remained little used for this species because vegetative propagation from cuttings was easy to perform, in contrast to other perennial fruit crops. Nevertheless in 1828, Lenoir cited already several advantages of this practice, including the adaptation to soil and climate conditions [6]. Phylloxera changed dramatically viticultural practices and grafting has been almost generalized in viticulture [1]. After vineyard recovery during the first decades of the XXth century, biological issues related to grafting and phylloxera resistance of American species slowly became neglected. The actual challenges in terms of pathogen and pest control and adaptation to climate change have recently renewed interest in phylloxera, rootstocks and grafting.

2. Historical findings

Grape phylloxera was first described in 1854 in the North America (New York) by the entomologist A. Fitch as being an aphid inducing galls on the leaves of different endemic *Vitis* species. It was named *Pemphigus vitifoliae*. In Europe, the first observations were made in 1863 near London under greenhouses where J.O. Westwood described the insect both on grapevine leaves and roots and named it *Peritymbia vitisana.* At the same time, first damages were reported in vineyards planted with *V. vinifera* in Pujaut (Gard, south-east of France), nearby a nursery run by the family Audibert, known to import American *Vitis* species. Grapevine decay rapidly expanded to surrounding places. One another outbreak was observed in 1867, close to Bordeaux by L. Laliman who grew American *Vitis* spp for several years. The problem became quickly so serious near the French south-east outbreak, that a field investigation was launched in 1868 under the request of local grower associations and politicians. The 15th July 1868, G. Bazille (winegrower and Chairman of the Central Society of Agriculture of Hérault), J.E Planchon (professor of Botany from the University of Sciences and Pharmacy of Montpellier) and F. Sahut (horticulturist) were the first ones to identify grape phylloxera insects feeding on roots of *V. vinifera* dying vines of Chateau de Lagoy (Bouches du Rhône, France). They suggested that this insect was the cause of the observed decay and named it *Rhizaphis vastatrix* (and quickly *Phylloxera vastatrix)*. In the following years, it was acknowledged that grape phylloxera was the cause of the decay (and not the consequence). Field and laboratory observations, made by growers and scientists both in France and in United States (at least L. Laliman, C.V. Riley, V.A. Signoret, J. Lichtenstein, J.E. Planchon) concluded that the different aphids described previously in United States of America, England and France were all identified as being the same species that was finally named *Daktulosphaera vitifoliae* [7]. The aphid-like insect and its complex life cycle (both subterrean and aerial depending on the *Vitis* host plant species) was later described in more detail by Cornu in 1878 [8] and Balbiani in 1884 [9]. More recently Granett *et al.* [10] published a review on the knowledge gathered during the XXth century and the genome sequence of grape phylloxera was released in 2020 [11].

Meanwhile the epidemy was quickly spreading in the south-east of France according to Duclaux (1874) [12]. In 1873, phylloxera was already present further north in the Rhone Valley (Drôme), further south-east towards Italy (Var) and further south west towards Spain (Hérault). The same situation occured nearby Bordeaux where grape phylloxera initially spread mainly towards north-east vineyards (Entre deux mers, St Emilion and Blaye). In 1877, it was present in all vineyard areas from Medoc to Sauternes [13]. An outbreak was also reported in Cognac region (Charente) in 1872. Then the epidemy moved up to the north of France, with 45 administrative departments contaminated in 1880, 52 in 1882, 60 in 1887, 69 in 1894 and all vineyard areas contaminated in 1900. Champagne was the last contaminated area [2]. Phylloxera reached most European and other viticultural countries in the world before the end of the XIXth century ([14]; Table 1, according to [2]).

Table 1. Dates of grape phylloxera outbreaks throughout the world.

Year	Country
1863	France
1865	Portugal
1871	Switzerland
1872	Austria
1873	California
1874	Germany
1875	Australia, Hungary
1877	Spain
1879	Italy
1880	South Africa, Serbia
1882	Romania
1885	Algeria
1888	Argentina
1893	Brazil
1898	Greece
1905	Tunisia

Considering the major threat caused by the progressive death of the vineyards, especially in the south of France, the French government launched in 1870 the "Superior Commission of Phylloxera" to evaluate all the possible means to solve the problem, and offered financial grants. Despite hundreds of proposals, no easy means to eradicate phylloxera was identified. The use of carbon sulphur and carbosulfonate of potassium by soil injection was initially highly supported (and funded) by the Commission, as the "sulfurist" approach. Despite the fact that these chemical treatments were expensive, dangerous, difficult to apply and not so efficient, up to 70000 ha were protected by this way, especially in high quality French vineyards, but also in Switzerland, Germany, Italy and in Algeria [1]. It was quickly observed that vineyards planted in sandy soils (<2-3% of clay) were not damaged by grape phylloxera. This observation supported the development of new vineyards in such soil types. Today it remains the only situation where own-rooted grapevine can be securely grown over a long period. Chandel *et al.* also reported that soil sand content was the most important parameter to characterize the risks of grape phylloxera development in own rooted vineyards in Washington state [15]. Soils made up of accumulations of volcanic ash (the Canary Islands, many areas in Italy, part of the Greek Cyclades, etc.) are also safe from phylloxera decay. The third most effective approach to control grape phylloxera was submersion under water during winter with the objective to kill the pest. It was first set-up by some growers in south of France as soon as 1870. Although it was very difficult to manage, required a lot of water and was only efficient in specific soil types, it was used on over 37000 ha in Languedoc and Bordeaux vineyards [1]. Today, the control of phylloxera populations in own rooted vineyards submitted to flood irrigation in Armenia and Argentina probably relay on the same principle [16]. However, this situation can change drastically in Argentina given the implementation of a drip irrigation system to face of global warming, which is increasingly adopted by winegrowers [17].

Initially the fact that American *Vitis* species, as suggested by L. Laliman, could be the solution was not considered too seriously. Several laws were voted in 1878 and 1879 to limit the transportation of American *Vitis* material to un-infected vineyards. However the advantages of these species in combatting grape phylloxera convinced quickly growers and scientists categorized as "the americanists" that this could be the solution. Most probably both L. Laliman and G. Bazille made concomitantly the same suggestion to graft sensitive European *V. vinifera* grapevines onto resistant American *Vitis* species. Although the "Superior Commission of Phylloxera" did initially not support this solution, a lot of efforts were made from 1870 to import, characterize and study the American plant material. The official scientific mission of J.E. Planchon to the United States in 1873 and, after 1874, the work of A. Millardet (professor at the University of Sciences from Bordeaux) both allowed us to increase considerably our knowledge of the American *Vitis* species and their various levels of resistance to grape phylloxera. Plantations of this material, most often *V. labrusca* hybrids, which were not highly resistant and not always adapted to the soil type, multiplied in the south of France, initially under the form of direct producers. This first stage of replantation was a bit anarchic and not always convincing. It may also have worsened the development of the epidemy and authorities were careful regarding these practices [18]. After 1880, grafting started to become the more general solution to adopt [1].

3. Grafting and the situation today

As mention above, grafting grapevine was not common before the phylloxera crisis, even if some growers such as L.C. Cazalis-Allut were already experimenting with this practice at large scale during the first half of the XIXth century [19]. J.E Planchon in 1874 [20] and A. Millardet in 1877 [21] had much expertise on American *Vitis* species and they supported very early grafting *V. vinifera* varieties onto American *Vitis* species, in addition to using them as direct producers to speed up the replantation of the destroyed vineyards [22]. Although the use of American *Vitis* species was excluded from grants by 1878-79 laws, it was clearly demonstrated in 1880-1881, that they were part of the solution to phylloxera and grafting started to develop. As an example, schools of grafting were organised in infected regions by local grower associations to train people and increase the capacity to produce grafted plants [23].

A. Milllardet [21], working with A. Fabre, a grower established close to Montpellier, was the first to analyse the resistance to grape phylloxera among wild American *Vitis* species and hybrids, to support that this trait was heritable through crosses and that the environment could affect it. He clearly established that *V. riparia* and *V. rupestris* were highly resistant at the root level and were the most interesting (at that time) genetic backgrounds for rootstocks because they had good rooting and grafting properties. He also excluded *V. labrusca*, which was described as sensitive. Later on, Ravaz in 1895 [24] and Boubals in 1966 [25] characterized in detail the level of resistance within a large diversity of *Vitis* species and accessions. Further results were provided by Ollat et al. [26]. Boubals also classified rootstocks and direct producers for phylloxera resistance [25]. Galet published a classification of *Vitis* accessions, rootstocks and direct producers for leaf galling sensitivity [2]. Although it was already introduced to France before grape phylloxera, the desirable traits of *V. berlandieri* (highly resistant to phylloxera and well adapted to calcareous soils) were recognised, especially after P. Viala (professor of Viticulture at the National School of Agronony in Montpellier, 1887) spent 6 month in United States in 1887 to collect promising accessions [27]. In 2023, Blois *et al.* analysed a large diversity panel of *V. berlandieri*, and characterized it molecularly and phenotypically [28]. Recent publications summarize the current knowledge about *Vitis* species used for rootstock breeding programs [26, 29, 30].

The first rootstocks used in Europe were hybrids from American species, imported to France before the introduction of grape phylloxera or to solve the powdery mildew problem. In France the first breeders (V. Ganzin, G. Couderc, P. Castel, A. Millardet, C. de Grasset, G. Foex) started to cross different American *Vitis* species, occasionally with *V. vinifera,* just before 1880. Many of the rootstocks still used today were obtained in the following decade. Rootstock breeding was initiated very quickly all over Europe and later on in the main grape growing countries (Table 2). Today, there are around 50 rootstocks commercially used worldwide [29, 31], but most of the grapes cultivated in the world are grafted onto very few rootstock genotypes [31]. In addition, most of them are derived from only three accessions of *V. berlandieri*, *V. riparia* and *V. rupestris*, which means a very narrow genetic diversity [32]. In France, replantation of vineyards with grafted grapevines was almost completed before the First World War [1]. Nowadays, more than 80% of the vineyards worldwide use grafted plants. Only in few countries or locations where grape phylloxera has not been introduced yet such as Cyprus or characterized by specific combinations of climate conditions and viticultural practices limiting its development, such as Washington state or Armenia, vineyards remain own rooted, but with the continuous threat of a grape phylloxera outbreak [15, 33].

Table 2. List of the most important rootstocks with the date of breeding, the name of the breeders and the country of obtention.

Year	Breeders and Rootstocks
1870-1879	L.Laliman : Viala (France) V. Ganzin : ARG1, ARG9 (France)
1880-1889	G. Couderc : 3309C, 161-49C, 1616C (France) A. Millardet : 101-14 MGt, 420 A, 41 B (France)
1890-1899	G. Foëx : 34 EM, 333 EM (France) Schwarzmann : 101 (Tchek republic) A. Ruggeri : 140Ru (Italy) F. Paulsen : 1103Pa, 775Pa (Italy)
1900-1919	P. Castel : 196-17Cl, 4010Cl, 216-3Cl (France) V. Malègue : 44-53Ma (France) Z. Teleki : 8B (Hungary) F.Kober : 5BB, 125AA (Austria) T.V. Munson : Dog Ridge, Ramsey (USA)
1920-1929	F. Richter: 99R, 110R (France) S. Teleki: 5C (Hungary)
1930-1959	JL. Vidal : BC2 (France, created in 1891 by M. Blanchard) Oppenheim: SO4, Binova (Germany)
1960-1969	J. Lafon: RSB1 (France, created most probably in 1896 by E. Resseguier)
1970-1979	Georgikon : 28 (Hungary) INRA: Fercal (France)
1980-1989	Geisenheim : Sori, Börner (Germany) INRA: Gravesac (France)
1990-2009	UCD: O39-16 (USA)
2010-	USDA: RS3, RS9 (USA) UCD: GRN1, 2, 3, 4, 5 (USA) INRA: Nemadex Alain Bouquet (France) Milan University : M1, M2, M3, M4 (Italy) Geisenheim HS : Libero, Vinto (Germany) Vitis Navarra : R8 (Spain)

As soon as it was considered as an efficient way to manage grape phylloxera and to adapt to various environmental conditions, several techniques of grafting were developed [34]. The objective was to find the most efficient practices in order to produce a high number of grafts with a high percentage of success. Field grafting on rooted rootstock cuttings or bench grafting techniques, initially by hand, and quickly with machines, were tested [35]. Field grafting has been mainly used in southern European vineyards where water is a limiting factor. This labour intensive practice that required more know-how was replaced by bench grafting in most vineyards. However with climate change, it seems to re-start in certain areas, even if it still represents a very small percentage of the total graft produced worldwide.

Although grapevine is generally easy to graft and grafting is widespread, the success rate is still around 50 to 60% with large differences between rootstock-scion combinations, grafting conditions, mother plant growing conditions and sanitary status, storage conditions of the wood, diameter of the cuttings, climatic conditions in nursery etc.. [36, 37]. Some authors consider that success rates depend on the grafting techniques. However most experimental results show that the processing rates and the technicity of workers rather than the grafting techniques by themselves affect the percentage of marketable grafts [38, Bloy et al., personal communication]. Few partial or full incompatibilities have been described in grapevine between scion and rootstock genotypes (reviewed by [39]). Some of them were explained by viral status of the cuttings [40], while the cause remains a mystery for other combinations [37]. Despite the fact that grafting has now been used for 150 years and that more or less 300 millions of grapevine grafts are produced annually worldwide, the scientific knowledge related to this practice remains scarce [41]. The complexity of graft union formation and the need for long term experiments results in controversies which are difficult to prove or disprove [42].

4. Some controversial points: sustainability of the resistance, grafting effect on production related traits and longevity

From the beginning, the development of grafting *V. vinifera* varieties onto American *Vitis* rootstocks was controversial. The first controversy was related to the sustainability of the resistance. So far, the current ability of *Vitis* species and rootstocks bred 150 years ago to control the development of grape phylloxera populations remains intact. Although this is still a matter of scientific questioning, more aggressive strains of phylloxera have been described in some vineyards around the world [43, 44, 45]. Then, the risk of resistance breakdown should not be neglected considering the narrow genetic diversity from which the rootstocks today were selected and the diversity of grape phylloxera strains in regard to aggressiveness. The reasons explaining the durability of this resistance over a so long period should be scientifically explored. The second controversy was that through grafting, the rootstock genotype could affect the properties of the *V. vinifera* varieties with some potential consequences on berry quality (the transmission of a foxy taste for example). Rigorous experiments demonstrated that it was not the case [35]. However these ideas are still a matter of debate [42]. Even if modern scientific approaches have demonstrated that rootstock and scion interact at the physiological level and exchange molecular information, recent experiments, made in countries where grape phylloxera is not a major issue (grafted and own rooted vines can be compared without the bias of grape phylloxera effects), did not show that own rooted vines were systematically less productive and vigorous than grafted vines [46, 47]. Finally a survey in different vineyards throughout the world did not show any negative effects of grafting on wine quality [48].

A third controversy was the possible reduction in the longevity of grafted grapevines. First of all, before considering this subject, a clear distinction has to be made between the age of a single vine and the age of a vineyard (duration between full replanting). In own-rooted vineyards, dead grapevines can be easily replaced by vegetative multiplication (provignage) from neighbour plants, which results in a constant regeneration. Such vineyards appear to last forever, but this is not true at the single plant level. As stated before, some incompatibilities between scion and rootstock genotypes exist, although this is not as common for grapevine as for other fruit species [5]. It can be a major issue when the incompatibility appears several years after planting, as occurs with the rootstock 161-49C [49]. Scientific studies regarding the cause of incompatibilities and the identification of early markers of this incompatibility should be a priority. It may also be argued that *V. vinifera* seems to be adapted to more variable environmental conditions and may develop a more vigorous root system. However grafted grapevines have been planted in many different environments with specific rootstocks selected to thrive in specific conditions. The ability of *V. berlandieri* crossed with *V. vinifera* to adapt to calcareous soils or the salt tolerance of *V. champinii* show that American *Vitis* species carry also genes for adaptation to abiotic stresses [26]. It has been suggested that diseases spreading through grafting are potentially responsible for the putative shorter longevity of grafted grapevines. Vineyard reconstitution after phylloxera crisis is associated with a large dissemination of grapevine fan leaf virus (GFLV). In addition to the cultivation of mother vines in contaminated locations and the massive multiplication of plant material necessary to replant most of the destroyed vineyards, there is some evidence that American *Vitis* species (and grafted grapevines) are very susceptible to GFLV while *V. vinifera* on their own roots are quite tolerant, GFLV being a very old virus from *V. vinifera* [50]. Nevertheless, virus diseases have also a strong economical impact on Australian vineyards, which are still largely own-rooted [51]. Concerning the Flavescence dorée phytoplasma, the main problem related to rootstocks is related to absence of symptoms on infected *Vitis* spp material growing in abandoned vineyards, which can be a source of primary infection [52]. Therefore they need to be carefully uprooted to limit disease dispersion.

Grafting is also considered as one of the many potential causes of the large decays associated with trunk diseases [36, 53]. It was shown that *Eutypa lata* and *Fomitiporia mediterranea* were never found in one-year canes used for grafting [54], but most fungi related to trunk disease were identified in young grafts after one year in nursery. Contamination could indeed occur during the grafting process or in nursery. However, there are still a lot unknown. Field experiments comparing herbaceous grafts (checked to be free of *Botryosphaeria* at planting) and classical hardwood grafts during several years showed no difference in contamination rate 4 years after planting and in symptom expression [55]. Trunk diseases are also reported in ungrafted vineyards in Chile and Australia [56, 57].

The fourth controversy is related to the reduction of varietal diversity, which would be linked to the development of grafting after the phylloxera crisis [58]. First of all, it has to be clear that varietal changes occurred at any time, mainly in order to respond to the wine consumption demand. For example, before the phylloxera crisis, Gouais blanc was replaced by Gamay, leading to the quasi-disappearance of this emblematic variety in commercial vineyards. It is true that grafting by itself induced the preferential development of some varieties that were more adapted to this practice, such as Cabernet-Sauvignon and Merlot, the replacement of some others as Folle blanche by Ugni blanc and Baco22A, and the strong reduction of Négrette because they appeared to be highly sensitive to Botrytis when grafted, probably an induced effect of conferred vigour. However, it has to be emphasised that grape phylloxera by itself was the first cause of the loss of biodiversity, mainly because of vineyard mortality. As written initially, 600000 ha disappeared and were not replaced, leading to the loss of many local varieties. This strong reduction of vineyard surface led to an important increase in demand, which resulted, in addition to fraudulent practices, in the plantation of more productive varieties such as Aramon and Carignan in place of Aspiran, Mourvèdre and Téoulier in the South of France. As a consequence of the huge disorganisation of the production system linked to grape phylloxera crisis, the Appellation system was created in France several decades later, to prioritise quality varieties, which also contributed to the loss of biodiversity. The development of the wine industry worldwide based on emblematic European varieties during the second half of the XXth century has also caused a major erosion of varietal diversity [59]. It is scientifically unfounded to state that grafting is the cause of every change (good or bad) that occurred after phylloxera crisis. Many changes in vineyard location or practices could be explained by other factors, such as the crisis by itself, the renewing of old vineyards, the drastic varietal changes or the modernization of agricultural techniques.

Based on these controversies, some people advocate the return of own rooted vineyards and/or the selection of new phylloxera resistant fruiting varieties (direct producers). It has to be remembered that grape phylloxera is still present in most vineyards and grafting onto resistant rootstocks is a way to cope with this pest, not to kill it. As stated previously, soils containing less than 2-3% clay are the only locations where own rooted vines can survive in an infected area. In all other areas, symptoms of decays induced by grape phylloxera appear usually 3 or 4 years after plantation and grapevines may become unproductive or die within 10 years. Except in very rare situations, where an exorbitant price can be obtained for wines produced with own-rooted, very low yielding vines, it not profitable for the vast majority of wine growers. Based on historical experience, chemical control or vineyard submersion appear to be unrealistic methods to control phylloxera at a large scale. Some biological control systems are under investigation to increase the lifespan of existing own rooted vines (see in § 5). Breeding new varieties resistant to several diseases and pests, including grape phylloxera, very adapted to abiotic stresses and characterized by high quality fruits, is a very attractive idea and an exciting objective for breeders, but also somewhat highly challenging and would not address the loss of genetic diversity. The actual knowledge regarding the genetic determinism of these traits and the modern biotechnological technologies (NBT for new breeding technology), such as genome editing or genomic selection, have increased the possibilities to obtain such a genotype. However gathering all the favourable traits in one single variety may take a long time and is a very expensive approach. According to Boubals [25], the genetic determinism of grape phylloxera resistance is complex and knowledge is still scarce (see in § 5). It is remarkable that resistance to grape phylloxera in existing rootstocks did not break down so far. This situation may be related to the fact that they are not resulting from many breeding cycles and consequently, the polygenic basis of phylloxera resistance maintains the combination of alleles selected in the wild types [60]. As a consequence, these "perfect" fruiting varieties remain a kind of dream, without forgetting that, beyond the tolerance to grape phylloxera, the use of rootstocks allows an important plasticity in terms of pedo-climatic and cultural adaptations. Practically grafting still is the most efficient, cheap and environmental-friendly sustainable solution to control grape phylloxera and to maintain diversity within the vineyards through rootstock-scion combinations. Therefore, rootstock breeding should be the preferred option with the objective to increase the genetic diversity used as parents, maintain an efficient phylloxera resistance and to improve the adaptation to biotic and abiotic edaphic stresses. Improving our knowledge about grape phylloxera resistance, interactions of roots with soil microbiome, properties of roots and adaptation to environmental issues, interactions between rootstock and scion, genetic determinism of these traits should be considered as scientific priorities.

5. Recent discoveries and studies

After the huge scientific activity associated with the study of grape phylloxera, the search for solutions, the characterization of American *Vitis* species and the development of rootstocks during the second half of the XIXth century, it is clear that these subjects were no longer priorities during the XXth century and were largely neglected. Since the turn of the XXIth century, new important findings have been published, which could improve our ability to develop a new range of rootstocks and define complementary solutions to control phylloxera.

5.1. Phylloxera genome and diversity

As mentioned previously, the sequence of the genome of phylloxera was released in 2020 [11]. This work demonstrated that grape phylloxera was introduced to Europe (France) from the upper Mississipi River in North American. Then it spread to the different countries in Europe, and from there to the rest of world. The French grape phylloxera populations have a molecular profile close to populations from the Mississipi River (Illinois, Wisconsin) and from New York, suggesting two distinct introduction events in South East and South West of France. Other European populations (Germany and Austria) are closer from those of Illinois, supporting an introduction from France. Profiles from the South American and Australia populations support also the hypothesis of an introduction from Europe. Some grape phylloxera biotypes have been reported to be able to induce nodosities on some rootstock roots. For example the rootstock Teleki 5C (*V. berlandieri* x *V. riparia*) was shown to be more sensitive to the phylloxera biotype G19 collected in Australia with a high number of nodosities and insect adults recorded on roots of 8 week-old potted cuttings [61]. Although it was stated from the first records during the XIXth century, that the most important trait associated to the resistance level of *Vitis* spp and hybrids is the formation of tuberosities on lignified roots, the potential breakdown of grape phylloxera resistance has to be monitored seriously.

5.2. Genetic determinism of the resistance to phylloxera

Boubals [25] was the first to publish a very complete study on the genetic determinism of phylloxera resistance in *Vitis* species. This study was based on the observation of more than 8000 hybrids from 57 crosses for their ability to develop root tuberosities. From this extensive work, it was concluded that phylloxera resistance is complex and under the control of several genes for all the resistant species. *V. vinifera* is carrying susceptibility genes in an homozygous form. There is a partial dominance for resistant genes from *M. rotundifolia*, *V. berlandieri*, *V. cinerea* and *V. rubra*. In some crosses between *V. vinifera* and *V. riparia*, *V. rupestris*, *V. labrusca*, *V. monticola*, *V. cordifolia* and *V. candicans*, there are some partial dominance of susceptibility. Phylloxera resistance of *M. rotundifolia* was further analysed by Bouquet in 1982 on approximatively 800 hybrids from several *M. rotundifolia* ($2n = 40$) × *V. vinifera* ($2n = 38$) crosses [62]. He suggested that *M. rotundifolia* root resistance to phylloxera was probably under the control of one major gene and three modifier genes. The major gene would be homozygous in *M. rotundifolia*, with partial dominance, located on a chromosome with a low pairing with its *V. vinifera* homologous chromosome. A recent molecular mapping study supports these assumptions [63]. A major QTL has been detected on LG7 from the Muscadine derived parent, and two additional ones on LG3 and 10. LG7 of the *Vitis* chromosome is known to be splitted in two in Muscadine (chr 7 and 20), which is in agreement with the low pairing chromosome hypothesis of Bouquet. A major locus was also identified for root galling in a *V. cinerea* x *V riparia* progeny, located on LG13 [64] and fine mapping of this QTL revealed a 202 to 403 kb region, depending on the haplotype, including 5 resistance genes in the *V. cinerea* haplotype [65]. Another root galling locus was identified within a *V. cinerea* × *V. vinifera* progeny on LG14 [66]. A mapping study performed on a progeny with various *Vitis* species backgrounds allow the identification of a major QTL for leaf galling also on LG14 and minor QTLs for root galling on LG5 and LG10 [67]. Fine mapping of the leaf galling LG14 QTL resulted in the identification of a 500 kb region which contains 36 resistance genes [68]. All together, these data support the complexity of the control of resistance to phylloxera. Further studies should be performed to identify the different genes in the various *Vitis* species. Genetic determinism of other traits such as rooting ability [28, 69], drought [70], limestone response [71] and salinity [72, 73] should also be investigated more actively.

5.3. Grafting and rootstock-scion interactions

As mentioned above, grafting success rates remain around 50% and there still a lot of unknown regarding the complex physiological processes related to graft union formation and incompatibility [39, 41]. In terms of gene expression changes, Cookson et al. reported the upregulation of genes related to cell wall synthesis as well as phloem and xylem development at the graft interface during the first stages of healing. Many genes induced by grafting were also induced during the activation of stem growth and metabolic activity in the spring [74, 75]. In addition, a large number of genes related to stress responses were upregulated at the interface in heterografts versus a homograft control. Similarly, grafting with compatible and incompatible scion clones showed that incompatibility was associated with the induction of genes regulating secondary metabolism and stress (and a range of other gene families [76]. This could suggest that the cells in these tissues can detect the presence of a non-self partner and this activates a defence response.

Identifying early markers of success in young grafts before plantation in nurseries would avoid an important waste of resources and time. However, the identification of these markers has proved difficult (as reviewed by Loupit and Cookson [41]). Carrere et al in 2022 attempted to use visual criteria to select good quality grafted grapevines with limited success [37]. Similarly, Tedesco et al studied the relationships between grafting success, callus formation, plant size and growth measurements, and fluorescence parameters [39]. In addition to visible criteria, molecular markers have also been studied [. Canas et al in 2014 suggested that gallic, caffeic, ferulic and sinapic acids, and catechin and epicatechin could be potential markers of graft incompatibility for certain clones of Syrah grafted onto the rootstock 110 Richter [77]. Similarly, Assuncao et al suggested that high concentrations of gallic acid, sinapic acid and catechin could be markers of poor compatibility in different clones of Tempranillo [76]. By studying a larger range of scion/rootstock combination, Loupit et al. in 2022 proposed that some biochemical compounds such as asparagine, transresveratrol, transpiceatannol and α-viniferin quantified at the graft interface one month after grafting could be used for this early detection of grafting success. However, they were much more informative in homograft [78] than heterograft combinations and had relatively poor predictive ability. This author then went on to analyse the spatio-temporal changes of the potential biomarkers of incompatibility at the graft interface [79]. A tissue-specific accumulation of metabolites at the graft interface was observed, for example, resveratrol accumulated in the damage xylem parenchyma, some other compounds such as naringenin and taxifolin are mainly present in new-formed callus cells. These tissue-specific metabolite accumulation patterns seem to suggest that metabolite markers are likely to reflect differences in the proportion of tissue types within a sample rather than responses to graft union formation *per se*., which will make the identification of reliable molecular markers challenging.

Even though it is clear that rootstocks do not modify the general characteristics of the *V. vinifera* scions, it would be false to say that there is no reciprocal effects of both genotypes. Understanding these interactions and identifying the underlying mechanisms are very important for the selection of the most performant scion/rootstock combination and to breed new rootstocks. As recently reviewed [81], scion effects seem to be predominant in most cases, except for some traits such as the petiole concentration of some mineral elements [82]. When analysing these interactions on a molecular basis, generally rootstock effects on the scion transcriptome are related to the scion phenotype (for example, poorly growing), but that transcriptomic differences between rootstock-scion combinations are usually not major [83, 84]. Globally hetero-grafting triggered an increase of gene expression in the scion shoot apex, with the most upregulated categories involved in DNA and chromatin modifications, suggesting potential epigenetic regulation, hormone and secondary metabolism, as well as receptor kinases involved in long distance defence response mechanisms [74, 81]. Small-RNA exchanges, potentially involved in epigenetic regulation, between scion and rootstock have been clearly demonstrated [85], providing new insights for understanding the interactions between partners.

5.4. Interactions with soil microbiome and possible complementary ways to control phylloxera

Plants, including grapevine, interact strongly with microorganisms, which could play a positive, negative or neutral role on their health and adaptation to the environment. Interactions with microbiome, and especially the soil one, has become a major field of scientific studies. Trouvelot *et al.* [86] and Darriaut *et al.* [87] have reviewed the current knowledge related to this subject. It has clearly been demonstrated that rootstock genotypes affect the rhizophere and root microbiota composition [88, 89]. In particular, Lailheugue *et al.* [90] showed that the rootstock genotype influences the diversity and the structure of the bacterial and fungal microbiome. Significant correlations were established between microbial variables and plant phenotype, such as the mineral status.

Among these soil microorganisms, it has been suggested for a long time that entomopathogen fungi could be useful to control grape phylloxera populations. Recently, the interest in *Metarhizium robertsii* was renewed, especially in countries as Australia and Argentina with a large majority of own-rooted vineyards in order to slow down a potential development of grape phylloxera [17]. If the ability of *M. robertsii* to parasite grape phylloxera eggs has been demonstrated *in vitro* and under controlled conditions [91, 92]. It was also shown that this fungus could colonize grapevine roots [93]. Its efficiency to control grape phylloxera population in the field on own rooted *V. vinifera* plants remain to be demonstrated and is currently under investigation.

6. Conclusions

The objective of this communication was to review some of the historical knowledge about the phylloxera crisis and the development of the grafting practice on American *Vitis* species and hybrids as a very efficient and nature-based solution, thanks to the extensive involvement of scientists in close collaboration with growers. Although this practice has some limitations, we have to admit that it has saved *V. vinifera*-based viticulture throughout the world. However, we have also to acknowledge that, once the problem of grape phylloxera appeared to be solved, this issue was almost forgotten, except when phylloxera outbreaks threatened own-rooted vineyards or not sufficiently phylloxera resistant rootstocks were used. Until recently, few scientific studies were performed on grape phylloxera genetics and biology, on the properties of American *Vitis* species, on rootstocks and on grafting. The lack of scientific interest in grape phylloxera as left some people to conclude “no news is good news” and that grape phylloxera has been eradicated definitively, however, this is not the case. Currently the development of new scientific techniques will allow us to answer new questions of grape phylloxera and provide new insights [94], but grafting remains the most efficient, cheap and sustainable way to control grape phylloxera (and other soil-borne pests like endoparasitic nematodes). Scientists must work to maintain this sustainability for the following decades, identify complementary practices and breed new rootstocks. Breeding multi-resistant scion varieties that could be grown on their own roots is considered as an elegant goal for geneticists and breeders. Nevertheless, we question whether it is worthwhile to invest much research effort in that direction as the advantages of independently selecting traits in the shoot and root genotypes are expanding the range of grafted plants used across agriculture today. In addition to the cost and time horizon, the major issues of resistance breakdown, varietal diversity and adaptation to the environment should be central to consider this option.

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