Volume 52 > Number 3 > 2018

Introduction to resistant vine types: a brief history and overview of the situation

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This article is published in cooperation with the 6th Oenoviti International Symposium New resistant grape varieties and alternatives to pesticides in viticulture for quality wine production held in Changins 16th may 2017.

Guests editors: Pierre-Louis Teissedre, Roland Riesen and Markus Rienth

Abstract

Today's breeding efforts applied to grapevines are mainly focused on the use of resistance to bio-aggressors, after being motivated, often unconsciously, for millennia by quantitative and qualitative concerns, and adaptations to environmental conditions. Thanks to advances in genomic knowledge and use of molecular markers, it is now possible to envisage more and more solutions against different pathogens (fungi, bacteria, viruses, insects), and in the near future, to ensure the durability of these resistances while combining them with resistance factors to abiotic stresses (drought, cold hardiness, soil conditions, etc.). This brief review presents the history and current situation of resistant vine types.

Keywords: genetic resistances, *Vitis*, breeding, bio-aggressors, abiotic stress

Received : 29 May 2018; Accepted : 29 May 2018; Published : 25 September 2018
doi:10.20870/oeno-one.2018.52.3.2220

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Introduction

Since the beginning of grapevine domestication, and until recent times (in the course of the 19th century), varietal improvement was generally the result of an unconscious approach. Concerning the *Vitis vinifera* species, this long process of selection is illustrated by the domestication syndrome, which refers to the observable morphological, physiological and cultural differences between the representatives of the cultivated (*V. vinifera* ssp *sativa*) and the wild (*V. vinifera* ssp *sylvestris*) subspecies (Lacombe, 2012). Thus, in the historical development area of viticulture, selection has empirically favored quantitative (yield, cluster size, flowering regularity, etc.) and qualitative characteristics (aromas, maturity period, berry color and shape, shoot behavior, etc.), applied to a species that had naturally evolved in the same environment. From the expansion of human travels initially motivated by trade and conquest (15th century), two phenomena successively occurred: transport of varieties from the Old World to the New, and then plant material moving from new lands towards the Old World. As a result of these different transports, *V. vinifera* was confronted with native foreign wild species, and with some pests and diseases it had never been brought into contact with, both in the new countries and on its native soil. The consequences were the occurrence and the inevitable development of serious diseases and parasites affecting *V. vinifera* in Europe (powdery mildew, downy mildew, phylloxera, black rot, etc.), and the failure of many attempts to cultivate varieties transplanted into a hostile environment.

First unintentional hybridizations

The unconscious use of genes for resistance to diseases was limited for a long time to the cultivation in the New World of varieties issued from American native species, probably mainly from *V. labrusca* (Pinney, 1989). In this context, the first involuntary interspecific hybridizations occurred in the vineyards cultivated by European settlers, in the eastern part of the North American continent. As such, Alexander N is considered as the first known hybrid, discovered in a vineyard near Philadelphia where James Alexander, gardener of the Penn's family, had previously planted cultivars of *V. vinifera* in 1683. The variety is considered as a natural crossing between *V. labrusca* and an unknown cultivar which may be from *V. vinifera*, in the same way as Isabella, Catawba or Concord, to cite a few varieties among the oldest known in North America. A recent publication has highlighted this hybridization phenomenon (Huber *et al.*, 2016): the analysis of simple sequence repeat (SSR) molecular markers established that Catawba N, which, according to Munson (1909), was discovered in a forest of North Carolina in 1801, was in fact derived from a seedling of Semillon B, the wild parent remaining unknown. The same study showed that Concord N is itself an offspring of Catawba N, crossed with another unidentified wild parent. These newly unveiled parentages confirm the assumptions that have been made for a long time.

Voluntary hybridization: a long and successful story?

While adaptation to abiotic factors is likely to have been a major and long-established focus of selection (phenology adapted to climatic zones, erected shoots facilitating cultivation, etc.), the deliberate choice of genotypes less sensitive to a disease started in Europe after the introduction of powdery mildew (reported in 1847). The parasite was probably introduced by cuttings of varieties imported from the United States and implanted as curiosities. Ironically, by pursuing these introductions in order to find resistant varieties to the threat (which was first called "the grapevine disease" in France), many deadly parasites penetrated and spread in Europe (phylloxera, downy mildew, black rot, etc.), with the well-known, considerable consequences.

At the same time (around 1840), and to complement the European varieties ravaged by fungal diseases, Brazil began to cultivate Isabella (hybrid of *V. labrusca*), which quickly spread into the country, along with other varieties such as Catawba, Concord or Delaware.

The research carried out in France in order to fight the terrible phylloxera (Garrier, 1989) has undoubtedly highlighted potentialities associated with the use of natural resistances against a major parasite. As early as 1869, Laliman in Bordeaux, having noticed the apparent resistance of the American varieties in his collection, had the idea of grafting the French grape varieties on some of them. This solution was finally adopted after years of experiments and controversies, and is still a remarkably effective and sustainable example of large-scale biological control of a major pest. The numerous interspecific hybridization works undertaken at that time allowed viticulture to be maintained in Europe and were focused on two aspects:

- Creation of rootstocks: resistance to phylloxera, first obtained using varieties originating from the United States (Noah, Jacquez, Herbemont, etc.), favored cultivars and crosses involving mainly *V. riparia* and *V. rupestris* species. But this base proved insufficient to cover the French (and European) needs in a context of wide variability of pedoclimatic conditions. In particular, resistance to the soil limestone, present in own-rooted *V. vinifera*, necessitated the introduction into the crosses of *V. berlandieri*, also adapted to drought, and then of *V. vinifera*.

- Creation of hybrid producers, own-rooted or grafted. Initially intended to replace the cultivars of *V. vinifera* while maintaining its traditional mode of propagation (rooted cuttings), numerous hybrids of increasing complexity were created with the objective of resistance to foliar diseases (mainly downy and powdery mildew). But the French hybrids failed to combine these multiple resistances in the same variety while ensuring a regular and qualitative production. Of all these witnesses to this era of creative expansion, and of the thousands that came out of the field trials and nurseries, only 20 varieties are still registered in the French Catalogue. Today, they represent about 8 000 ha in the French vineyard, after peaking at more than 400 000 ha in 1958.

However, the beginnings of intentional hybridization took place in the United States, early in the 19th century. Prince (1830) wrote that he had practiced 10 000 seedlings (of which there is no trace afterwards), and named in his treatise 91 native American grapevine varieties, among which "Pond's seedling" may be the first cultivar to bear the name of its creator (William Pond). Other hybridizers carried out works that sometimes involved grape varieties of *V. vinifera* (Valk, in 1845, Allen, Munson, Jaeger, etc.). In France, Victor Ganzin was the first to follow this path from 1877, soon followed by Couderc, Seibel and many others.

Today, the legacy of these ancient hybrids is considerable. The use of rootstocks is a worldwide success, and brings much more than the single tolerance to phylloxera which motivated the first works. Many hybrids or their progeny are used in difficult areas in Eastern Europe or North America (USA and Canada) where their resistance to winter frost is appreciated. This is the case for Vidal 256 B, Frontenac N, or La Crescent B for example. In Brazil, table varieties such as Isis Rg, or varieties for the production of grape juice are issued from numerous hybridizations, involving multiple genitors and allowing production in an environment that is very favorable to fungal diseases. Some complex hybrids are commonly used in the breeding programs, where they bring the resistances inherited from many American and few Asian species (Riaz *et al.*, 2013).

The use of other genetic resources: the cases of *Vitis amurensis* and *Muscadinia rotundifolia*

In order to take advantage of the resistance to severe frosts of this species (some cultivars can withstand temperatures close to -40°C), breeders have used *V. amurensis* for improvement, especially in Russia (Potapenko since 1936), China, Hungary, Ukraine, the former Yugoslavia, Germany, etc. Later, the genetic mechanisms of cold resistance have been confirmed (Xu *et al.*, 2014), and three loci of resistance to downy mildew have been discovered (*Rpv8*, Blasi *et al.*, 2011; *Rpv10*, Schwander *et al.*, 2012; and *Rpv12*, Venuti *et al.*, 2013). The species was also found to be resistant to *Agrobacterium tumefaciens* (crown gall), whose tumors can be a serious problem in cold winter areas (Szegedi and Kozma, 1984).

Several genotypes were subsequently used in different modern breeding programs (beginning in the 1970's), including pyramiding programs favored by France (INRA ResDur; Schneider *et al.*, 2014) or work carried out in Italy (University of Udine). We can cite mainly the varieties Bronner B, Solaris B or Kozma 20-3.

The high resistance of *M. rotundifolia* to numerous parasites justified several attempts to cross this species with *V. vinifera* since 1871 in the United States (Galet, 1988 for a review). The first ones were unsuccessful due to chromosomal differences between the *Vitis* (2n = 38) and *Muscadinia* subgenera (2n = 40). However, in 1919, Detjen obtained viable but not very fertile hybrids by crossing Malaga seedling no. 1 with *M. rotundifolia*. One of these F1 varieties, coded NC6-15, was used in 1974 in France by Alain Bouquet, who carried out six series of consecutive backcrosses with different varieties of *V. vinifera*, which resulted in numerous genotypes put into experimentation from 2006.

Some of these cultivars were used as genitors for subsequent INRA programs (ResDur) aimed at pyramiding resistance to the two main fungal diseases in France. To date, three series of crossings made it possible to obtain varieties possessing two loci of resistance to both powdery and downy mildew ("ResDur 1 and 2"), and three loci for each of the "ResDur 3" series. The French strategy is to ensure the sustainability of resistances by creating a varietal assortment combining several major and combined sources of resistance to these two parasites.

In addition, the resistance of *M. rotundifolia* to soil-borne nematodes was studied in France (INRA; Bouquet and Danglot, 1983) and in the United States (Davidis and Olmo, 1964), which resulted in the registration of the rootstock Nemadex Alain Bouquet in France (Ollat *et al.*, 2011) and 039-16 in the United States (Walker *et al.*, 1991). Work in this direction is still ongoing. For example, in France, the "Remunex" project aims to evaluate the resistance to transmission of fanleaf in a progeny of *M. rotundifolia* × *V. vinifera* (Esmenjaud, personal communication).

Resistances to other diseases and pests

The study of the mechanisms of resistance to downy and powdery mildew led to the discovery of numerous loci with varying levels of efficacy (*Vitis* international variety catalogue (VIVC) website for a review; http://www.vivc.de/). Until recently, however, such mechanisms were unknown for other fungal diseases, with less economic impact on viticulture.

The presence of several quantitative trait loci (QTLs) of resistance to downy and powdery mildew in the genome of a variety does not provide cross-resistance with other fungal parasites, which can reveal themselves very harmful when not controlled by treatments against major diseases. In European vineyards, black rot (*Guignardia bidwellii*) is probably the most problematic of these fungi. Therefore, the discovery of two loci carrying resistance to black rot in the Börner rootstock (*V. riparia* × *V. cinerea*; Rex *et al.*, 2014) opened the way for a use in future breeding programs. The interest of this approach has recently been confirmed by a screening of many kinds of genotypes, which determined the presence of high-level resistance in several interspecific hybrids and in a seedling from the species *M. rotundifolia* (Hausmann *et al.*, 2016).

In the future, it is likely that other fungal diseases considered today as secondary problems (rotbrenner, anthracnose, phomopsis, etc.) make a remarkable comeback in vines planted for their resistance to the main diseases and cultivated without fungicide spraying. With the durability of the mechanisms of resistance, their observation is one of the tasks assigned to the future French resistance observation network ("Oscar") that will support the spread of these varieties, and will try to anticipate the situations considered to be at risk.

The tricky problem of trunk diseases

Many studies have highlighted the importance of the varietal factor in the development of these different decays (ex. Grosman and Doublet, 2012). In particular, the French variety Savagnin B, its mutants, and most of its numerous offspring whose behavior is known, appear among the most problematic cultivars, which suggests the existence of hereditary factor(s). In order to study the segregation of susceptibility to trunk diseases, a population of seedlings from self-fecundation of Savagnin B was generated in France (Le Cunff, personal communication). The evaluation of these genotypes, based on the indirect measure of fungi aggressiveness in the wood, is still being acquired. But such studies will certainly be long, concerning diseases with slow progression and few validated model tests.

Resistance to Pierce's disease (bacteria Xylella fastidiosa)

Following the work carried out at the University of Davis (California), the discovery of a locus for resistance to Pierce's disease in *V. arizonica* (named *PdR1* and associated with genetic markers; Krivanek *et al.*, 2006), made it possible to obtain by breeding and molecular marker-assisted selection a certain number of tolerant genotypes, of which 5 to 10 could be soon available for the grape growers. However, the question arises about the durability of such a resistance conferred by a single gene. Another question concerns the introduction to the vineyard of plants able to carry the bacteria without expressing any symptoms. Such reservoirs of the pathogen could represent a significant danger to other vines, and contribute to the worsening of the epidemic in case of efficient propagation by the vectors. This is exactly the same problem with the flavescence doree disease in France, with a new research program trying to explore susceptibility differences between cultivars (Malembic *et al.*, 2018).

Conclusion: future prospects

As pointed out, many varietal programs are focused on resistance to aggressors. This priority approach corresponds to society's expectations (limitation of phytosanitary inputs), as well as to obvious economic realities. However, the new varieties will have even greater potential (and long-term prospects for the future) if they combine (durable) resistance with major pests, adaptations to climatic constraints, production corresponding to qualitative and quantitative objectives and factors of competitiveness (easy cultivation, longevity of the vineyards, etc.). For example, researches for grapevines and rootstocks on the genetic determinism of drought tolerance (eg. Marguerit *et al.*, 2014) are promising. However, the ideotypes to reach are complex, and combine many disjointed characteristics; future varietal creations will have to propose acceptable compromises between the different priorities. The extremely quick development of knowledge related to the genome and its regulation should make it possible in a near future to offer researchers and breeders more and more efficient tools to achieve these multiple objectives.

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