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ISBN 978-3-030-99406-8 ISBN 978-3-030-99407-5 (eBook)
https://doi.org/10.1007/978-3-030-99407-5

This Springer imprint is published by the registered company Springer Nature Switzerland AG
The registered company address is: Gewerbestrasse 11, 6330 Cham, Switzerland

Foreword

Grapevine rootstocks are an essential feature for sustainable viticulture around the world. Only a few grape-growing regions are spared infestation by phylloxera, and pests and diseases of grapevine roots challenge production nearly without exception. Since the introduction of phylloxera into Europe, the subsequent eruption of phylloxera in European viticulture, and the distribution of phylloxera very widely, the value of rootstocks in viticulture has been firmly appreciated and rootstocks steadily and increasingly recognized as critical for successful viticulture. Those who seek to maximize vine performance through rootstocks should understand the attributes and origin of rootstocks and how the characteristics of rootstocks may influence scion performance and vine adaptation.

This book describes the importance, utilization, and future of rootstocks in the context of grapevine botany, plant breeding, and horticulture. The early years of the phylloxera crisis saw pioneering research with many North American grape species selections and their hybrids, both as rootstocks and in direct production. That research was fueled by crisis and the exigency of identifying practical approaches for phylloxera management. Rootstocks developed in that first wave of research are still in use, and the fundamental biological and viticulture knowledge of phylloxera/rootstock/scion interactions guides further developments and investigations. Yet now, a more comprehensive understanding of *Vitis* species, their origins, relationships, and attributes informs viticulture, grape breeding, and the utilization of rootstocks.

We recognize that the North American grape species that coexist with phylloxera in nature show adaptations to reduce phylloxera damage, such as resistance and tolerance to the pest. Many questions about the ecology and evolution of grapevines and their pests and pathogens are relevant to species research and rootstock utilization and breeding. How does natural gene flow among grape species and populations influence interactions with phylloxera and other pests? Why does resistance and tolerance against pests and diseases with a delimited original distribution exist in grape species native to other areas? How stable is the resistance and tolerance of our rootstocks against pests and diseases that must infest to order to survive? How does the use of rootstocks shift pest and disease populations? In vineyards, phylloxera and other pests often encounter a genotypical monoculture, yet in nature, dioecy and vegetative propagation in this long-lived liana engender a mosaic of genetic diversity.

The chief role of rootstocks in viticulture is to provide protection against pests and diseases of the vine roots, with phylloxera protection the keystone. Other pests and pathogens, including fungi, bacteria, and nematodes, have long been recognized as important threats, and rootstocks that protect against them are increasingly the goal of breeding and evaluation programs. Is phylloxera vanquished? Hardly! Rather, protection against other pests and pathogens is taking its place alongside phylloxera protection as pest and pathogen populations shift with changing environments, management practices, and production regions. We now have the germplasm and evaluation methods to develop and introduce rootstocks that provide protection against crown gall and ground pearls, and more pest and disease protection is revealed as investigations continue. We can and must reduce pesticide applications to vineyards by using protective rootstocks instead.

Rootstocks have an important and emerging place in the management of grapevine virus diseases. Fanleaf degeneration and other diseases associated with nematode-transmitted viruses now may be managed with rootstocks that are resistant to nematodes or that provide protection against the diseases themselves. Yet, the mechanism and genetic drivers of this protection against virus diseases are poorly understood, which slows progress in breeding and introducing rootstocks with adaptation to diverse soils and climates. Rootstocks influence the development of leafroll disease and other virus-associated grapevine diseases, and the deployment of leafroll disease resistance and tolerance in rootstocks that provide protection against phylloxera and other pests would be an important step in harm reduction. Rootstocks and their progenitor species will be a source of genetic resistance and tolerance against virus disease protection for scion variety improvement.

While a handful of rootstock varieties dominate the global grapevine nursery trade, extensive and diverse breeding and evaluation programs continue to create and characterize rootstocks with superior adaptation to specific environments and varieties and which provide protection against newly emerging pests and diseases as well as against recognized threats. The movement of grape plant material in a secure phytosanitary context is an important contributor to the adoption of rootstocks. Similar growing conditions may favor the utilization of the same rootstocks in different regions for similar benefits, and familiarity both with well-established rootstocks and new rootstock variety introductions is essential. Shared trends drive shared needs–water use efficiency, yield efficiency, sodium and chloride tolerance, and adaptation to acidic and calcareous soils are valued in many areas, and rootstocks that provide special value must be introduced widely.

Through our familiarity with the species, their phenotypic characteristics, and their horticultural contributions increase steadily, new frontiers and opportunities are presented by technologies such as recombinant DNA technology, gene editing, somatic hybridization, doubled haploids, and synthetic seeds that are as yet incompletely realized in rootstock improvement and utilization. Botanical exploration and analysis reveal distinctions and relationships among species and populations, with newly recognized distinct types to be expected even in well-described habitats and with new Neotropical species on the horizon. From this book, future initiatives in grape rootstock breeding, horticulture of grape rootstock evaluation and use, and grape species research will be inspired.

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Preface

The genus *Vitis* includes approximately 80 different species of grapevines, depending on the subtle shifts in taxonomic classification taking place as natural hybridization and ongoing classification efforts continue to evolve. Of all species in the genus *Vitis*, the European grape, *Vitis vinifera*, is certainly the most important worldwide for the commercialized cultivation of table, raisin, and winegrapes. Grape species other than *V. vinifera* have also historically been used in the making of juices, wine, jellies, and jams. Many of these wild grape species have nutraceutical properties and health benefits that have drawn consumer attention and contributed to interest in incorporating them into breeding programs beyond the traditional efforts of rootstock hybridization from wild species.

Initially, *V. vinifera* was propagated asexually and without the common day practice of grafting to wild species hybrids. In the late nineteenth century, an aphid-like pest, phylloxera (*Daktulosphaira vitifoliae*), an aphid-like pest, was inadvertently introduced from North America to Europe and ultimately impacted most grape-growing regions worldwide. Phylloxera causes damage by feeding on the structural roots of *V. vinifera*, eventually leading to vine death. In an effort to save the wine industry, American *Vitis* species which coevolved with phylloxera were eventually used as rootstocks for the widely planted *V. vinifera* scion cultivars. The use of wild species directly as a rootstock has become a common practice. Later, crosses between these wild species became common, and historical breeding efforts led to the modern grape rootstock breeding programs currently active around the world. Today, grape rootstocks play a fundamental role in resistance to biotic and abiotic stresses and adaptation of grapevine to different environmental conditions, a factor that has opened commercial grape growing up to regions that might otherwise be overlooked. Grape rootstocks can be used for adaptation to a variety of soil conditions, including soil texture, depth, nutrient availability, pH, salinity, lime content, water availability (drought), and water drainage. Rootstocks can also be used to shift scion cultivar the timing of various key phenological events and indirectly affect vineyard design.

Regardless of the specific rootstock selected or the environmental challenge addressed, it is necessary to introduce new rootstocks using resistance advantages from different species. There are around 1500 grape rootstocks developed in the world, of which around 50 are commonly used as commercial rootstock. North American species account for around 30 species, and two-third of them have already been used for rootstock breeding. However, it has been reported that the most commonly available rootstocks are derived from just three American species *(V. berlandieri, V. rupestris,* and *V. riparia).* Therefore, the most common grape rootstocks have a narrow genetic base, and efforts to extend the gene pools for breeding programs by using the other species are of ongoing importance to the industry and scientific community.

This book will annotate about 20 grape species that are vitally important in breeding programs and provide information on approximately 150 of the most familiar grape rootstocks in the world.

A great deal of research has been performed on grape rootstocks around the world. However, the resources and information are scattered, inaccessible, and unexploitable for the vast majority of grape growers and researchers. In this book, we have made substantial efforts to gather and classify this information and combine it with our own opinions and experiences in the hope that it will be useful to those interested and accessible to a broad audience. Various sources included in the text required permission and copyright approval. As such, we spent substantial time on this critical issue. It is necessary to thank all the authors, researchers, institutions, and associations for their help and cooperation. Some of the resources were particularly difficult to source and it would not have been possible to include them without the support of the corresponding authors and their contacts. This book is the result of the dedicated efforts of all of them. We hope that all faculties, researchers, and specialists will help us improve the quality of the book in future editions by sending comments to us.

Petersburg, Virginia, USA — Alireza Rahemi
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About the Authors

Dr. Alireza Rahemi is Postdoctoral Research Associate at Virginia State University, USA. He has done extensive research and continues to work on wild relatives of subtropical and temperate fruits and nut trees. He worked as a Horticulture Specialist at the Ministry of Agriculture in Iran. He received his Ph.D. in Horticulture and conducted part of his research at University of Florida, USA. His Ph.D. research was focused on wild almond species, including genetic diversity using new emerging molecular techniques. He has also conducted research on the wild grape species of Southern Ontario and their utilization as rootstock during his postdoctoral research at the University of Guelph, Canada.

Dr. Jean C. Dodson Peterson is Associate Professor of Viticulture at California Polytechnic State University, San Luis Obispo. She earned her undergraduate degree from the University of California, Davis, in Viticulture and Enology with a minor in Managerial Economics. She continued at UC Davis, earning her M.S. and Ph.D. in Horticulture and Agronomy. She teaches basic viticulture, the advanced viticulture series, advanced independent study, senior project research, and thesis courses. She has been awarded the Panhellenic Award for Excellence in Education and the Terrance Harris Award for Excellence in Mentorship. She has also earned her Certification in Effective College Instruction from the Association of College and University Educators and the American Council on Education. Her research program strives to advance the understanding of grapevine physiology, rootstock–scion interactions, rootstock selection, and vine performance factors. Her research mission is to execute innovative and inspiring research that advances the wine and viticulture industry and scientific community.

Dr. Karl True Lund is University of California Viticulture Advisor for Madera, Merced, and Mariposa Counties. The primary research he is currently conducting is looking at the adaptation of nematode-resistant rootstocks for high yielding mechanized vineyards. Prior to his current position, he was Lecturer at California Polytechnic State University San Luis Obispo, where he taught introductory viticulture and viticulture pest management classes. He conducted his Ph.D. work at the University of California at Davis. His Ph.D. work looked at the diversity of phylloxera within California. He also assessed the resistance of wild accessions and current rootstocks to the different types of phylloxera he identified within the state.

Chapter 1
Introduction

Grape cultivation is considered to be as old as civilization (OIV 2017). Today, grape-derived products are one of the most economically important fruit crops (Wen et al. 2018), with more than 10,000 grape varieties grown in 100 countries, on an estimated 7.5 m ha, with approximately 75 m tons of production each year (OIV 2017). Most production occurs in the zone between 30° and 50° latitude in the northern and southern hemispheres (Stevenson 2005).

Around 50% of world grape production is used to make wine (wine grapes), with 33% eaten as fresh fruit (table grapes), and the remaining 17% used as raisins, juice, or stored in the form of grape musts (freshly crushed fruit) whether concentrated or not (FAO-OIV 2016; OIV 2017). Most commercial production is with pure *Vitis vinifera* (Christensen 2003). 'Kyoho', 'Cabernet Sauvignon', 'Sultanina', 'Merlot', 'Tempranillo', 'Airen', 'Chardonnay', 'Syrah', 'Red Globe', 'Garnacha Tinta'/'Garanche noir', 'Sauvignon blanc', 'Pinot noir'/'Blauer burgunder', and 'Trebbiano toscano'/'Ugni blanc' are, in sequence, the varieties with the highest production and they cover more than one-third of the planted area (OIV 2017). 'Kyoho', a Concord-like cross popular in East Asia, is the most commonly planted variety by acreage (OIV 2017). It is not pure *V. vinifera*; however, it still owes more than 50% of its parentage to *V. vinifera* (VIVC 2019). The initial reason for the wide adoption of rootstocks was, and in many locations still is, due to phylloxera (*Daktulosphaira vitifoliae*), an aphid-like pest of grapevines. Phylloxera is native to the Eastern portion of North America and was inadvertently imported into the wine-producing regions of France in 1860 (Skinkis et al. 2009). By the end of the nineteenth century, France had lost more than 70% of its wine production (Robinson and Harding 2016). The French wine industry was historically based on the exclusive use of own-rooted *V. vinifera*, which has no resistance to root-feeding by phylloxera. However, some American *Vitis* species had co-evolved with phylloxera and thus had evolved tolerance to the pest. The use of hybrids between French *V. vinifera* varieties and American *Vitis* species failed to produce a variety that was resistant to phylloxera while also being considered to produce wine of commercially acceptable quality. The French wine industry eventually succeeded in addressing phylloxera by grafting

A. Rahemi et al., *Grape Rootstocks and Related Species*,
https://doi.org/10.1007/978-3-030-99407-5_1

French wine varieties (as scions) onto an American *Vitis* species, or species hybrid, as a rootstock. As phylloxera spread from France to virtually every wine-growing region worldwide, so did the use of rootstocks (Campbell 2004). The first rootstocks were simply selections of individual wild American *Vitis* species, some of which are still used today. The two initial American species utilized as rootstocks were *Vitis riparia* and *Vitis rupestris*. Rootstocks derived from these two species were initially successful but eventually declined in France's lime-rich soils as neither tolerated calcareous conditions. As a result, *Vitis berlandieri* was collected from America and incorporated into rootstock breeding programs in an effort to convey lime tolerance. Lime, however, was not the only abiotic soil condition that rootstocks must address. Over time, soil characteristics such as texture, drainage, salinity, and pH have all been addressed or attempted to be addressed through rootstock selection. Furthermore, biotic issues other than phylloxera have also required the use of rootstocks to address properly. Specifically, the control of nematodes has fallen mainly to rootstocks for control, an issue that is complex given the vast array of resistance levels across the various commercial rootstocks (Ferris et al. 2012).

In addition to dealing with issues in the soil and soil pests, rootstocks have been shown to affect scion growth (vigor) and yield (Keller et al. 2008; Kidman et al. 2014b; Nelson 2015; Dodson Peterson and Walker 2017), nutrition status (Holzapfel and Treeby 2007; Lambert et al. 2008; Kidman et al. 2014a), pollination, and fertilization efficacy (Kidman et al. 2014a), and berry characteristics and fruit chemistry (Rühl et al. 1988; Koundouras et al. 2009; Migicovsky et al. 2021). Expansion of grape production into new areas, development of new cultivars, and increasing concerns about adapting grapevines for changing climates continue to necessitate the use of wild grapevine species in breeding programs (Klein et al. 2018). An understanding of the effects a rootstock will have on a scion must start with an understanding of species parentage. Each American *Vitis* species, as well as the other grape species used in rootstock breeding, has a specific set of traits. They are possessing a basic understanding of the traits particular species have or are likely to have assisted in informing what traits might be observed in the newly bred progeny. The majority of rootstocks in use today are hybrids of three species: *V. berlandieri*, *V. riparia,* and *V. rupestris* (Galet 1998; Whiting 2005; Ollat 2016). Riaz et al. (2019) used 21 nuclear and 14 chloroplast markers to show that the relationship of many of these rootstocks is even closer. Twenty-six of the common rootstocks bred between the 1890s and 1930s had at least one parent coming from only three specific selections: *Vitis berlandieri* cv.Rességuier 2, *V. rupestris* cv. du Lot and *V. riparia* cv. Gloire de Montpellier. Overall, the results indicate that 39% of the genetic background of the major analyzed rootstocks originated from *Vitis berlandieri* cv. Rességuier 2, *V. rupestris* cv. du Lot and *V. riparia* cv. Gloire de Montpellier. The results found that the world's existing rootstocks have a narrow genetic base derived from only a few American grape species (Riaz et al. 2019). Lesser-known components of grapevine evolutionary biology include relationships among species that are used as rootstocks (e.g., *V. cinerea* var. helleri, *V. riparia*, *V. rupestris*). Hybrids between *V. cinerea* var. helleri and *V. riparia* or *V. rupestris* have been used to produce rootstocks that are easy to propagate, and that can withstand challenging abiotic conditions (Galet

1979). Single nucleotide polymorphisms (SNPs) used for a phylogenomic study in *Vitis* demonstrate that these important rootstock species occur in different clades within the North American subgenus *Vitis*. *V. cinerea* is most closely related to *V. vulpina*, while *V. riparia* and *V. rupestris* form a clade together with *V. acerifolia* (Miller et al. 2013). In general, the common grape rootstocks used today encompass around 20 different grape species. It is here where the industry must focus and advance understanding in order to make the most progress with future breeding efforts.

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