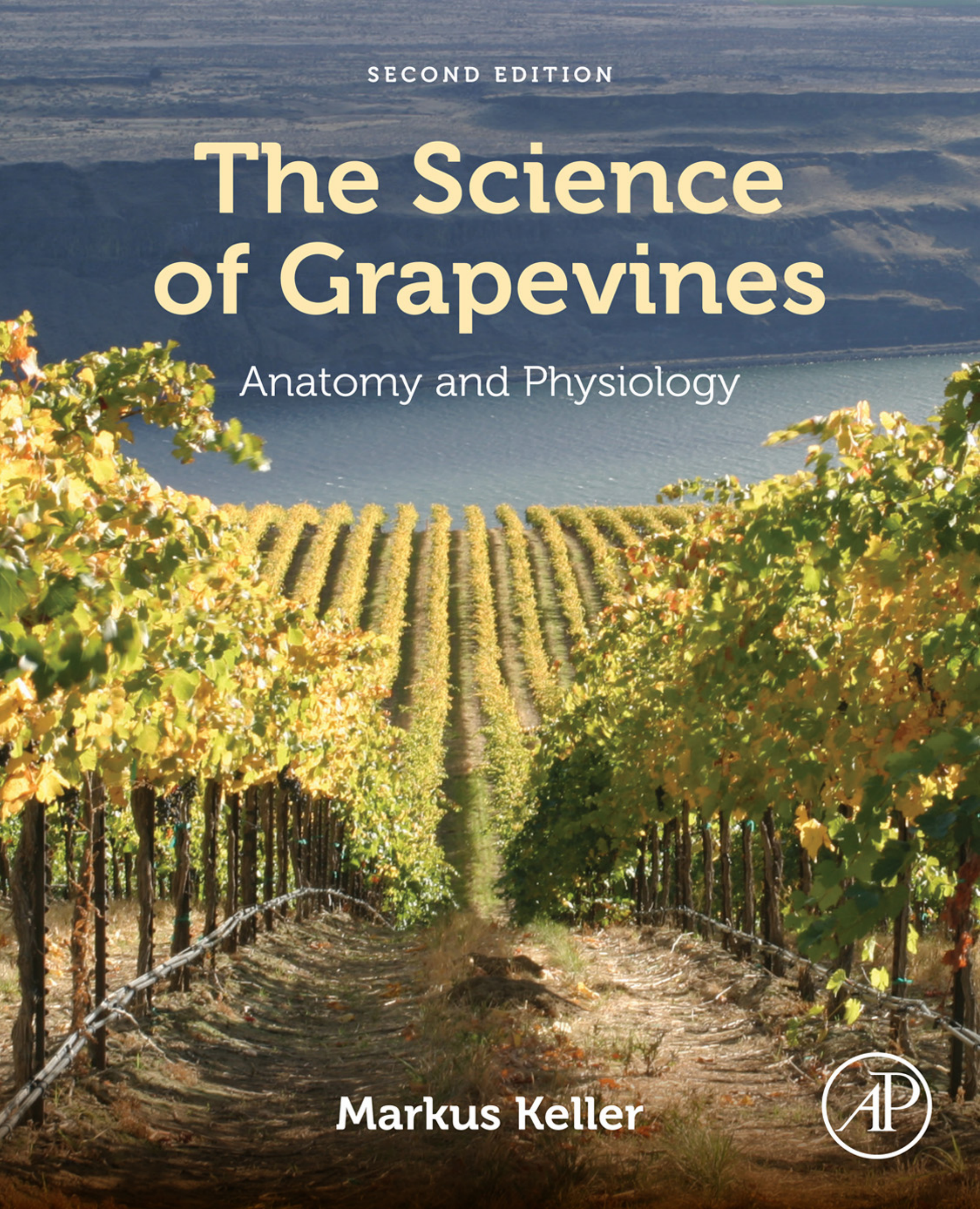
SECOND EDITION

The Science of Grapevines

Anatomy and Physiology



Markus Keller

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Second Edition

Markus Keller
Irrigated Agriculture Research and Extension Center,
Washington State University, Prosser, WA,USA

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About the Author

Markus Keller is the Chateau Ste. Michelle Distinguished Professor of Viticulture at Washington State University's Irrigated Agriculture Research and Extension Center in Prosser. He received his master's degree in agronomy (plant science) in 1989 and a doctorate in natural sciences in 1995 from the Swiss Federal Institute of Technology in Zürich. Having grown up on a diversified farm that included wine grape production among other crops and livestock, he began his research and teaching career in viticulture and grapevine physiology at the Federal Research Station for Fruit-Growing, Viticulture and Horticulture in Wädenswil (now Agroscope Changins-Wädenswil), Switzerland. He then moved to Cornell University in Geneva, New York, and from there to Charles Sturt University in Wagga Wagga, Australia, before coming to eastern Washington. In addition, he has been a regular guest lecturer at the Universidad Nacional de Cuyo in Mendoza, Argentina. He was awarded the Swiss AgroPrize for innovative contributions to Switzerland's agriculture industry. His research focuses on developmental and environmental factors, as well as vineyard management practices, as they influence crop physiology and production of wine and juice grapes.

Preface to the Second Edition

It has been 5 years since *The Science of Grapevines* was first published. Science (Latin *scientia* = knowledge), or the pursuit of knowledge, does not stand still, of course, which poses a challenge for any printed textbook. For the second edition, I have reviewed and integrated novel material in an attempt to present the latest information available from the scientific literature. Additionally, several gaps have been closed by revisiting some of the older, classic literature. The task has not been trivial; the second edition contains more than 750 additional literature references. All chapters have been thoroughly revised and updated. The former large and diverse Chapter 7 has been split: the new Chapter 7, "Environmental Constraints and Stress Physiology," is now focused on responses to abiotic stress, whereas the new Chapter 8, "Living with Other Organisms," addresses responses to biotic stress. Abstracts have been added, summarizing the key points of each chapter in a highly condensed manner. To help readers unfamiliar with specific terminology, a glossary is now included that explains many chemical, anatomical, physiological, and viticultural terms that appear throughout the text. The new list of abbreviations and symbols will provide further assistance in navigating the text.

Grapes were among the first fruit species to be domesticated and remain the world's most economically important fruit crop. According to the Food and Agriculture Organization of the United Nations, grapevines were planted on almost 7 million hectares producing more than 67 million metric tons of fruit in 2012. More than 70% of this crop was used to make wine, 27% was consumed as fresh fruit (table grapes), 2% was consumed as dried fruit (raisins), and less than 1% was processed to grape juice, distilled to brandy, or transformed into vinegar.

The Science of Grapevines explores the state of knowledge of the construction and life of this economically and socially vital plant species. The book is an introduction to the physical structure of the grapevine, its various organs and tissues, their functions, their interactions with one another, and their responses to the environment. It focuses essentially on the physical and biological functions of whole plants rather than the metabolism and molecular biology of individual cells. It is nonetheless necessary to review some fundamental processes at the cell, tissue, and organ levels in order to build up an appreciation of whole-plant function. The book covers those elements of physiology that will enhance our understanding of grapevine function and their implications for practical vineyard management. Although of necessity the text contains a plethora of technical terms and details, I have tried to resist the temptation to dwell in biochemical and molecular-biological jargon. Most physiological processes (water movement through the vine's hydraulic system and evaporation through plant surfaces may be exceptions) are rooted in biochemistry. They are driven or at least facilitated by enzymes which, in turn, are built based on blueprints provided by genes. I have therefore taken it for granted that it is understood that a developmental process or change in chemical composition implies a change in enzyme activity, which in turn implies a change in the activity, or expression, of one or more genes. This does not imply, as used to be thought, that "one gene makes one enzyme," or that "one enzyme makes one chemical," but means merely that all enzymatic processes are rooted in the dynamic expression of certain genes.

Many biochemical and biophysical processes apply to many or even all plants. Perhaps no process is truly unique to grapevines. Chances are if grapes employ a solution to a survival issue, then some or many other species do the same thing, because they share a common ancestor that invented the trick a long time ago. For example, microbes hit upon photosynthesis and respiration long before these discoveries enabled some of them to join forces and evolve into plants. Consequently, although this book is about grapevines, and primarily about the wine grape species *Vitis vinifera*, I have borrowed heavily from research done with other plant species, both wild and cultivated, perennial and annual, woody and herbaceous, including that "queen of weeds"—at least in the fast-paced world of modern molecular biology—*Arabidopsis thaliana*, the otherwise inconspicuous thale cress. I have even taken the liberty of borrowing insights gained using microorganisms such as the yeast *Saccharomyces cerevisiae*, which gives us the wine, beer, and bread that enable us to think about these issues.

This book aims to be global in scale. It covers topics ranging from the physiological aspects of tropical viticulture near the equator all the way to those that pertain to the production of ice wine at the temperate latitudinal margins of grape growing. It moves from vineyards at sea level to vineyards at high altitude. It considers the humid conditions of cool, maritime climates, the moist winters and dry summers of Mediterranean climates, as well as the arid environment, often combined with hot summers and cold winters, typical of continental climates in the rain shadows of massive mountain ranges. Yet a book of this nature is necessarily incomplete, and so is the selection of published information included in the text. No one can read everything that has been and is being published, even in the admittedly relatively narrow field of grapevine anatomy and physiology. The magnitude of the task of reviewing as much of the pertinent literature as possible often forced me to rely on review papers where they were available. I apologize to those friends and colleagues whose work I did not cite or cited incompletely or incorrectly. Science—and scientists—can only ever hope to approximate the truth. This and the simple fact of "*errare humanum est*" will guarantee a number of errors throughout the text. These are entirely my responsibility, and I would be grateful for any feedback that might help improve this book and further our understanding of the world's most important and arguably most malleable fruit crop. After all, the full quote from Seneca the Younger, who was a contemporary of Columella, the Roman author of agriculture and viticulture textbooks, reads "*errare humanum est, sed in perseverare diabolicum*" ("to err is human, but to persevere is devilish").

As with the first edition, many people have made large and small contributions to bring this second edition to fruition. I am indebted to all of these generous individuals. My wife, Sandra Wran, has supported this project throughout and also waited countless long weekends for me to "finish" reading another paper or revising another section. Many of the illustrations were skillfully drawn by Adrienne Mills, and Lynn Mills helped with data collection and some of the most recalcitrant illustrations. Feedback from colleagues and students has helped to eliminate numerous mistakes, some of them more glaring than others. I am also grateful for the encouragement from Nancy Maragioglio and Carrie Bolger at Elsevier, who were always quick to answer my questions *du jour*.

CHAPTER

BOTANY AND ANATOMY

1

CHAPTER OUTLINE

ABSTRACT

The diverse species of grapevine belong to the botanical family Vitaceae, which includes mostly shrubs and woody lianas that climb using leaf-opposed tendrils. The vast majority of the thousands of grape cultivars belong to the species *Vitis vinifera*. Some of the other species are used as pest-tolerant rootstocks to which cultivars with desirable fruit properties are grafted. Cultivars are propagated asexually as cuttings so that each individual is a clone of its mother plant. Grapevines comprise vegetative organs (roots, trunk, cordon, shoots, leaves, and tendrils) and reproductive organs (clusters with flowers or berry fruit). All organs are interconnected through the vascular system comprising the xylem for water and nutrient transport, and the phloem for assimilate transport. The roots form the plant—soil interface, while the trunk, cordons, and shoots of a vine form its stem. The shoots carry the leaves, buds, tendrils, and clusters. Leaves are arranged in spiral phyllotaxy in juvenile vines and in alternate phyllotaxy in mature vines. Buds are young, compressed shoots embedded in leaf scales. Tendrils and clusters are modified shoots. After fertilization, the flower pistil develops into the berry fruit. The berry comprises up to four seeds surrounded by the endocarp, the mesocarp or flesh, and the exocarp or skin.

Keywords: Bud; clone; cultivar; grape berry; leaf; root; rootstock; shoot; tendril; *Vitis*

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1.1 BOTANICAL CLASSIFICATION AND GEOGRAPHICAL DISTRIBUTION

The basic unit of biological classification is the species. According to the "biological species concept," a species is defined as a community of individuals—that is, a population or group of populations whose members can interbreed freely with one another under natural conditions but not with members of other populations (Mayr, 2001; Soltis and Soltis, 2009). In other words, such communities are reproductively isolated. Although each individual of a sexual population is genetically unique, each species is a closed gene pool, an assemblage of organisms that does not normally exchange genes with other species. Their genes compel the individuals belonging to a species to perpetuate themselves over many generations. Yet all life forms on Earth are interrelated; they all ultimately descended from a common ancestor and "dance" to the same genetic code, whereby different combinations of three consecutive nucleotides of each organism's deoxyribonucleic acid (DNA) specify different amino acids that can be assembled into proteins. Because they are thus interrelated, organisms can be grouped according to the degree of their genetic similarity, external appearance, and behavior. In the classification hierarchy, closely related species are grouped into a genus, related genera into a family, allied families into an order, associated orders into a class, similar classes into a division (plants) or a phylum (animals), related divisions or phyla into a kingdom, and, finally, allied kingdoms into not an empire but a domain. The "evolutionary species concept" recognizes this ancestor–offspring connection among populations that may follow distinct evolutionary paths to occupy separate ecological niches but may continue to interbreed for some time (Soltis and Soltis, 2009). For example, although they have been geographically isolated for over 20 million years, Eurasian and North American *Vitis* species are still able to interbreed readily.

As is the case with many plants, the species of the genus *Vitis* are not very well defined because of the extreme morphological variation among and within populations of wild vines (Currle et al., 1983; Hardie, 2000; Mullins et al., 1992). This implies the following: (i) all *Vitis* species are close relatives that share a relatively recent common ancestor and (ii) evolution is still at work, throwing up new variants all the time (see Section 2.3). Many vine species are actually semispecies—that is, populations that partially interbreed and form hybrids under natural conditions, which is in fact common among plants and may be an important avenue for the evolution of new species (Soltis and Soltis, 2009). Despite some hybridization where their natural habitats overlap, however, the various *Vitis* gene pools usually stay apart so that the populations remain recognizably different. Nonetheless, species that occur in close proximity are more similar than distant species in similar habitats. Grapevines are a good example of the limits of taxonomic systems, demonstrating that there is a continuum of differentiation rather than a set of discrete, sexually incompatible units. As early as 1822, the Rev. William Herbert asserted that "botanical species are only a higher and more permanent class of varieties," and in 1825 the geologist Leopold von Buch postulated that "varieties slowly become changed into permanent species, which are no longer capable of intercrossing" (both cited in Darwin, 2004). A few decades later, Charles Darwin expressed it clearly: "Wherever many closely allied yet distinct species occur, many doubtful forms and varieties of the same species likewise occur" and, furthermore, "there is no fundamental distinction between species and varieties," and, finally, "varieties are species in the process of formation" (Darwin, 2004). Indeed, modern genetic evidence indicates that the various *Vitis* species evolved relatively recently from a common ancestor so that they have not yet had time to develop the complete reproductive isolation that normally characterizes biological species. Thus, *Vitis* species are defined as populations of vines that can be easily distinguished by morphological traits, such as the anatomy of their leaves, flowers, and berries, and that are isolated from one another by geographical, ecological, or phenological barriers; such species are termed *ecospecies* (Hardie, 2000; Levadoux, 1956; Mullins et al., 1992). The following is a brief overview of the botanical classification of grapevines, starting with the domain at the top of the hierarchy and finishing with a selection of species at the base.

Domain Eukaryota

All living beings, making up the Earth's biological diversity or biodiversity, are currently divided into three great domains of life: the Bacteria, the Archaea, and the Eukaryota. The Eukaryota (eukaryotes; Greek *eu* = true, *karyon* = nucleus) include all terrestrial, sexually reproducing "higher" organisms with relatively large cells (10–100 μm) containing a true cell nucleus, in which the DNA-carrying chromosomes are enclosed in a nuclear membrane, and cell organelles such as mitochondria and plastids (Mayr, 2001). They evolved following injections of oxygen into the atmosphere caused by abiotic (i.e., nonbiological) factors such as plate tectonics and glaciation (Lane, 2002). The vast majority of life and the bulk of the world's biomass—the small (1–10 μm), single-celled prokaryotes (Greek *pro* = before) with cell walls composed of peptidoglycans (protein–polysaccharides)—is grouped into other two domains. However, both the photosynthetic organelles (chloroplasts, from cyanobacteria) and the "power plants" (mitochondria, from proteobacteria) of eukaryotic cells have descended from (symbiotic) bacteria that "infected" other single-celled organisms (or were "swallowed" by them) over 1 billion years ago. These organelles still retain some of their own DNA (i.e., genes), although more than 95% of their original genes have since been and are still being lost or transferred (donated) to their host's nucleus (Timmis et al., 2004; Green, 2011). The mitochondria, in turn, have acquired a sizeable fraction (>40%) of genes from the chloroplasts, which may have returned the favor by incorporating some mitochondrial genes (Goremykin et al., 2009). Genetic modification or transformation, resulting in transgenic organisms, is evidently a natural process. Some bacteria cause diseases of grapevines; for example, crown gall is caused by *Agrobacterium vitis* and Pierce's disease by *Xylella fastidiosa* (see Section 8.2).

Kingdom Plantae

The Eukaryota comprise at least five major lineages that are termed supergroups or kingdoms (Green, 2011); the number and associations change as the relationships among organisms become better known. The Plantae have a haplo-diploid life cycle and cell walls composed of cellulose, and are studied in the field of Botany. This supergroup includes the plants and the green and some other algae. There are approximately 500,000 plant species, which are classified into 12 phyla or divisions based largely on reproductive characteristics. The higher or vascular (Latin *vasculum* = small vessel) plants, to which grapevines belong on account of their water conduits, form the subkingdom Tracheobionta (Greek *trachea* = windpipe). The Animalia comprise the multicellular, diploid (having two sets of chromosomes) animals with cells lacking cell walls, except in arthropods (insects, spiders, and the like) which have chitin cell walls, and are the domain of Zoology. The Fungi include the haploid (having one set of chromosomes) mushrooms, molds, and other fungi, with cell walls composed of glucans and chitin; they are studied in Mycology. Because they are more closely related to each other than to any other eukaryotes, the animals and fungi are now grouped together into the Opisthokonta (Green, 2011). Whereas one group of fungi (singular fungus), the yeasts (especially *Saccharomyces cerevisiae*), turns grapes into wine through fermentation, other fungi cause diseases of grapevines (see Section 8.2); for example, gray rot is caused by *Botrytis cinerea* Pers.:Fr. and powdery mildew by *Erysiphe necator* (a.k.a. *Uncinula necator* (Schwein.) Burr.). Animals also can be important pests of grapevines, especially certain insects (e.g., phylloxera, *Daktulosphaira vitifoliae* Fitch), mites, and nematodes. The number and names of the other lineages and the relationships among them remain contested; they include all other "higher-order" organisms, from single-celled microbes or microorganisms (Greek *mikros* = small), including some that resemble unicellular fungi, plants (some algae), and animals (protozoans), to large, multicellular seaweeds (marine algae such as kelps).

Division (phylum) Angiospermae (synonym Magnoliophyta)

The angiosperms (or, in new terminology, the magnoliophytes) are the flowering plants, which include perhaps as many as 400,000 species. They are believed to have evolved from a common ancestor that lived approximately 160 million years ago during the late Jurassic period, and they make up the most evolutionarily successful group of plants. Angiosperms are the plants with the most complex reproductive system: They grow their seeds inside an ovary (Greek *angeion* = pot, vessel) that itself is embedded in a flower. After the flower is fertilized, the other flower parts fall away and the ovary swells to become a fruit, such as a grape berry. Indeed, the production of fruits is what defines the angiosperms and sets them apart from the gymnosperms, with whom they are classed in the superdivision Spermatophyta, or seed plants.

Class Dicotyledoneae (synonym Magnoliopsida)

This class is large and very diverse, and its members are often called dicot plants. The vast majority of plants (~200,000 species), including most trees, shrubs, vines, and flowers, and most fruits, vegetables, and legumes, belong to this group. Like all members of the Dicotyledoneae, grapevines start their life cycle with two cotyledons (seed leaves) preformed in the seed.

Order Rhamnales (Vitales according to the Angiosperm Phylogeny web)

Grapevines belong to the order Rhamnales, which gets its name from the genus *Rhamnus*, the buckthorns. The order has three families: Rhamnaceae (e.g., *Ziziphus jujuba* Mill., jujube tree), Leeaceae (the oleasters), and Vitaceae. Plants of the family Leeaceae are more recognizable as being related to grapevines than those belonging to the Rhamnaceae, being shrubs or trees with flowers aggregated in inflorescences, black berries, and seeds that resemble grape seeds, also named pips. Some taxonomists have now separated the Vitaceae (Jansen et al., 2006) and Leeaceae from the Rhamnales and placed them in the order Vitales.

Family Vitaceae

The members of this family are collectively termed grapevines. The family contains approximately 1000 species assigned to 17 genera that are typically shrubs or woody lianas that climb by means of their leaf-opposed tendrils—hence the name Vitaceae (Latin *viere* = to attach). Although most species of this family reside in the tropics or subtropics, a single species from the temperate zones has become the world's leading fruit crop grown in almost 90 countries for wine and juice production or as fresh table grapes or dried grapes (raisins). Vitaceae roots are generally fibrous and well branched, and they can grow to several meters in length. The leaves are alternate, except during the juvenile phase of plants grown from seeds, and can be simple or composite. The fruits are usually fleshy berries with one to four seeds. All cultivated grapes belong to either the genus *Muscadinia* ($2n = 40$ chromosomes) or the genus *Vitis* ($2n = 38$ chromosomes). The former classification of *Muscadinia* and *Euvitis* as either subgenera or sections of the genus *Vitis* has fallen out of favor among taxonomists (Mullins et al., 1992). Because of the different numbers of chromosomes, crosses between these two genera rarely produce fertile hybrids. Key morphological characteristics of the two genera include the following:

- simple leaves
- simple or forked tendrils
- generally unisexual flowers—that is, either male (staminate) or female (pistillate)
- fused flower petals that separate at the base, forming a calyptra or "cap"
- soft and pulpy berry fruits.

Genus *Muscadinia*

Members of the genus *Muscadinia* usually have glabrous (hairless) leaves, simple tendrils, non-shredding bark, nodes without diaphragms, and hard wood (Currle et al., 1983; Mullins et al., 1992; Olmo, 1986). Because they do not root from dormant cuttings, they are usually propagated by layering, although they do root easily from green cuttings. The "homeland" of this genus extends from the southeastern United States to Mexico. The genus has only three species, which are all very similar and may not even deserve to be classed as separate species (Currle et al., 1983; Mullins et al., 1992; Olien, 1990).

- *Muscadinia rotundifolia* Small (formerly *Vitis rotundifolia* Michaux): A dioecious plant, although breeding has yielded perfect-flowered and female cultivars, such as Noble, Carlos, or Magnolia, known as "muscadines," that are grown as table, jelly, or wine grapes (Olmo, 1986). The species is native of the southeastern United States. The musky flavor and thick skins of the fruit can be unattractive. The species has coevolved with and therefore resists or tolerates, albeit to varying degrees, the grapevine diseases and pests native to North America, including the fungi powdery mildew and black rot (*Guignardia bidwellii* (Ellis) Viala and Ravaz), the slime mold downy mildew (*Plasmopara viticola* (Berk. and Curtis) Berl. and de Toni), the bacterium causing Pierce's disease, the aphid phylloxera, and the dagger nematode *Xiphinema index* (which transmits the grapevine fanleaf virus), but is sensitive to winter freeze and lime-induced chlorosis (Alleweldt and Possingham, 1988; Olien, 1990; Olmo, 1986; Ruel and Walker, 2006). Although usually incompatible in both flowering and grafting with *Vitis* species, it does produce fertile hybrids with *V. rupestris*, which allows it to be used in modern (rootstock) breeding programs.
- *Muscadinia munsoniana* Small (Simpson): Native to Florida and the Bahamas, with better flavor and skin characteristics than *M. rotundifolia*, but not cultivated.
- *Muscadinia popenoei* Fennell: Native to southern Mexico ("Totoloche grape"), relatively unknown.

Genus *Vitis*

The genus *Vitis* occurs predominantly in the temperate and subtropical climate zones of the Northern Hemisphere (Mullins et al., 1992; Wan et al., 2008a). All members of this genus are perennial vines or shrubs with tendril-bearing shoots. This genus probably comprises 60–70 species (plus up to 30 fossil species and 15 doubtful species) spread mostly throughout Asia (~40 species) and North America (~20 species) (Alleweldt and Possingham, 1988; Wan et al., 2008b,c). The Eurasian species *Vitis vinifera* L. gave rise to the overwhelming majority of grape varieties cultivated today. Plants that belong to this genus have hairy leaves with five main veins, forked tendrils, bark that shreds when mature, nodes with diaphragms, and soft secondary wood. They all can form adventitious roots, a trait that permits propagation by cuttings, yet only *V. vinifera*, *V. riparia*, and *V. rupestris* root easily from dormant cuttings. Although the ancestor of all *Vitis* species may have had perfect (i.e., bisexual or hermaphroditic) flowers (McGovern, 2003), the extant wild species are dioecious (Greek *dis* = double, *oikos* = house), containing imperfect male (i.e., female sterile or staminate) or female (i.e., male sterile or pistillate) flowers on different individual plants, whereas the cultivated varieties of *V. vinifera* have perfect or, in a few cases, physiologically female flowers (Boursiquot et al., 1995; Levadoux, 1956; Negrul, 1936; Pratt, 1971; see also Figure 1.1). Members of this genus are very diverse in both habitat and form. Nevertheless, all species within the genus can readily interbreed to form fertile interspecific crosses called hybrids, which implies that they had a relatively recent common ancestor. Moreover, all *Vitis* species can be grafted onto each other. The genus is often divided into two major groups: the American and the Eurasian groups. The dominant species of the two groups differ greatly in their useful agronomic traits (Table 1.1), which makes them attractive breeding partners (Alleweldt and Possingham, 1988;

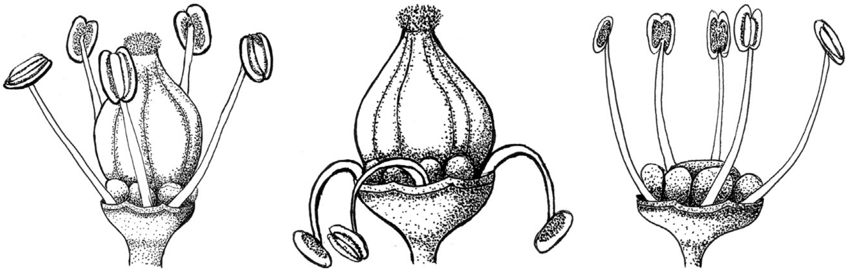

FIGURE 1.1

Flower types in the genus *Vitis*: perfect flower (left), female flower (center), and male flower (right).

Illustrations by A. Mills.

Table 1.1 Broad Viticultural Traits of American and Eurasian Grapevine Species

Trait	Eurasian Species	American Species
Fruitfulness	Good	Poor or highly variable
Fruit quality	Good	Poor
Usefulness	Highly diverse products	Niche products, rootstocks
Propagation capacity	Good	Variable
Lime tolerance	Good	Highly variable
Phylloxera tolerance	Poor	Good or variable
Disease resistance	Poor	Good or variable

This et al., 2006). Unfortunately, none of the many attempts and thousands of crosses that have been tested to date have truly fulfilled the breeders' hopes of combining the positive attributes while eliminating the negative ones contained in the natural genetic variation of the two groups. Perhaps the genes conferring disease resistance are coupled to those responsible for undesirable fruit composition. Indeed, hybrids have often been banned in European wine-producing countries because of their perceived poor fruit (and resulting wine) quality. Confident predictions of the future availability and spread of newly bred cultivars in the New World (Olmo, 1952) have been wrecked by the reality of taste conservatism of producers and consumers alike. The only unequivocal success story thus far has been the grafting of phylloxera-susceptible European wine grape cultivars to rootstocks that are usually hybrids of tolerant American *Vitis* species (see Section 1.2).

American group

Depending on the taxonomist, this group contains between 8 and 34 species, of which several have become economically important as wine or juice grapes. Because of their varying resistance to the North American grapevine diseases and pests, members of this group are also being used as rootstocks (see Section 1.2) or crossing partners in breeding programs (Alleweldt and Possingham, 1988; This et al., 2006). As an aside, crosses are always listed as maternal parent × paternal parent (i.e., the mother's name comes first). The species of this group generally have thinner shoots with longer internodes and less prominent nodes than the Eurasian species. They also have smaller buds, and the leaves have very shallow sinuses and often a glossy surface. All grape species native to North America are strictly dioecious (i.e., none of them has perfect flowers), and most of them grow near a permanent source of water, such as a river, stream, or spring (Kevan et al., 1985, 1988; Morano and Walker, 1995; Figure 1.2). Following is an incomplete list and brief description of some of the more important species. Much of this information is derived from the Plants Database (plants.usda.gov) of the United States Department of Agriculture Natural Resources Conservation Service:

- *Vitis labrusca* L.: Vigorous climber ("northern fox grape") native to the eastern United States from Georgia to southeastern Canada, with Indiana as its western limit. This species differs from all others in that it usually has continuous tendrils, that is, a tendril at every node. Some of its cultivars (e.g., Concord and Niagara) are commercially grown in the United States for juice, jam, jelly, and wine production. Nonetheless, these cultivars (which, unlike wild *V. labrusca*, have perfect flowers) are of mixed *V. labrusca* and *V. vinifera* descent; they probably arose through natural hybridization, and thus have been classed as *Vitis* × *labruscana* L. Bailey (Mitani et al., 2009; Mullins et al., 1992; Pratt, 1973; Sawler et al., 2013). The distinct foxy flavor (caused by methyl anthranilate) that characterizes this species is popular in the United States but strange to Europeans. The species is cold tolerant, resistant to powdery mildew and crown gall, and tolerant of phylloxera. It is, however, susceptible to downy mildew, black rot, and Pierce's disease and has poor lime tolerance, preferring acid soils. Hybrids of *V. labrusca* were exported to Europe at the beginning of the nineteenth century. Some of these plants carried powdery mildew, downy mildew, black rot, and phylloxera, which drove most populations of wild vines extinct and brought the European wine industry to the verge of destruction.
- *Vitis aestivalis* Michaux: Vigorous climber native to eastern North America, growing in dry upland forests and bluffs. It is very cold hardy (to approximately −30°C) and drought tolerant, tolerates wet and humid summers as well ("summer grape"), and is resistant to phylloxera,

FIGURE 1.2

The “bank grape,” *Vitis riparia*, growing in a forest in upstate New York (left) and the “canyon grape,” *Vitis arizonica* Engelmann, growing up a riverside tree in Utah’s Zion National Park (right). Note the large size of the wild vines and the long “trailing trunks” at the bottom right.

Photos by M. Keller.

powdery and downy mildew, and Pierce’s disease. The species is very difficult to propagate from cuttings. Its fruits are used to make grape jelly, and the cultivars Norton and Cynthiana are commercially grown as wine grapes in the southern and midwestern United States (Tarara and Hellman, 1991). It seems likely, however, that the two names are synonyms for the same cultivar and that they are hybrids between *V. aestivalis* and *V. labrusca* and/or *V. vinifera* (Reisch et al., 1993; Sawler et al., 2013).

- *Vitis riparia* Michaux: Widespread in North America from Canada to Texas and from the Atlantic Ocean to the Rocky Mountains. This species climbs in trees and shrubs along riverbanks (“bank grape”) and prefers deep alluvial soils, but does not do well in calcareous soils (i.e., prefers acid soils), and its shallow roots make it susceptible to drought—a trait it also confers on the rootstocks derived from its crosses with other species. It is the earliest of all the American species to break buds and ripen its fruit, matures its shoots early, is very cold hardy (to approximately −36°C), is tolerant of phylloxera, and is resistant to fungal diseases but susceptible to Pierce’s disease.
- *Vitis rupestris* Scheele: Native to the southwestern United States from Texas to Tennessee, the species is now almost extinct. It is found in rocky creek beds (“rock grape”) with permanent water, and it is vigorous, shrubby, and rarely climbs. It has deep roots for anchorage but is not very drought tolerant on shallow soils, and its lime tolerance is variable. The species tolerates phylloxera and is resistant to powdery mildew, downy mildew, and black rot, but susceptible to anthracnose (*Elsinoë ampelina* (de Bary) Shear).

- *Vitis berlandieri* Planchon: Native to central Texas and eastern Mexico, this species climbs on trees on deeper limestone soils between ridges. It is one of very few American *Vitis* species that have good lime tolerance. Its deep root system makes it relatively drought tolerant, but it is very susceptible to waterlogging. The species breaks buds and flowers much later than other species and is the latest ripening of the American group with very late shoot maturation. It is somewhat tolerant of phylloxera and resistant to fungal diseases and Pierce's disease, but it is very difficult to propagate and to graft (Mullins et al., 1992).
- *Vitis cinerea* Engelmann: Sprawling, vigorous, but relatively low climber native to much of the southeastern United States through Texas. It thrives in moist woodlands and near streams and prefers relatively acid soils. The species is resistant to powdery mildew.
- *Vitis candicans* Engelmann: Very vigorous climber native to the southern United States and northern Mexico. The species is drought tolerant, relatively tolerant of phylloxera, and resistant to powdery and downy mildew and Pierce's disease, but it is difficult to propagate. Other southern species, such as *V. champinii* Planchon and *V. longii* Prince, are probably natural hybrids of *V. candicans*, *V. rupestris*, and other native species (Pongrácz, 1983). They are highly resistant to nematodes.

Eurasian group

There are approximately 40 known species in this group, most of them confined to eastern Asia. Chinese species are particularly diverse, growing in the dry southwest, the northern and southern foothills of the Himalayas, the very cold northeast, and the hot and humid southeast. Although some of them are resistant to fungal diseases and may tolerate high humidity (Li et al., 2008; Wan et al., 2007, 2008a), most of these species are little known, and there may be several additional species that have not yet been described. Most Eurasian species are not resistant to the North American grapevine diseases, and yet one of them has come to dominate the grape and wine industries throughout the world.

- *Vitis vinifera* L.: Native to western Asia and Europe between 30°N and 50°N, but temporarily confined, in more or less isolated populations, to the humid and forested to arid, volcanic mountain ranges of the southern Caucasus between the Black Sea and the Caspian Sea and to the Mediterranean region during the Ice Ages (Grassi et al., 2006; Hardie, 2000; Levadoux, 1956; Maghradze et al., 2012; Zohary and Hopf, 2001). This is the most well-known species of the Eurasian group, as it gave rise to most of the cultivated grapes grown today. The species is highly tolerant of lime, even more so than *V. berlandieri*, and drought. Because the cultivated grapevines have hermaphroditic or, rarely, physiologically female flowers, they are often grouped into the subspecies *V. vinifera* ssp. *sativa* (also termed *V. vinifera* ssp. *vinifera*). But according to many taxonomists, *V. vinifera sativa* is merely the domesticated form of *V. vinifera* (ssp.) *sylvestris*. According to this view, the differences between the two forms are the result of the domestication process (Levadoux, 1956; This et al., 2006), that is, they arose through human rather than natural selection. However, the concept of subspecies (or geographical races) as taxonomically identifiable populations below the species level ought to be abandoned, as it is highly subjective and inefficient and, therefore, biologically meaningless (Wilson and Brown, 1953).
- *Vitis sylvestris* (or *silvestris*) (Gmelin) Hegi: Native to an area spanning central Asia to the Mediterranean region, this group contains the dioecious wild vines (also termed lambrusca vines)