

Chapter 10

Crop Wild Relatives of Grape (*Vitis vinifera* L.) Throughout North America



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Abstract Although cultivated grapevines (*Vitis vinifera* L.) were domesticated from their closest relative in Central Asia, grape wild relatives from North America are vital due to their use as grafted rootstocks. Rootstocks derived from North American *Vitis* species are critical to the global wine, table, and raisin grape industries for resistance to the root pest phylloxera (*Daktulosphaira vitifoliae*). These rootstocks can also provide other benefits such as cold and drought tolerance, nematode and disease resistance, and control over vigor and phenology. Phylogenetic studies of the many *Vitis* species native to North America often disagree on the number of species and their boundaries, specifically in the Southwestern United States and Mexico. The wild vines are all dioecious and, with the exception of subgenus *Muscadinia* Planchon, interfertile – allowing for interspecific hybridization wherever ranges overlap. A better understanding of the relationships between North American *Vitis* species is needed to identify gaps in the current ex situ germplasm collections. Additionally, efforts must be made to safeguard dwindling populations of some species in their native environments. Conservation of these valuable genetic resources will ensure that grape breeders throughout the world have the necessary diversity to adapt to a changing environment.

Keywords Crop wild relatives · Grapevine breeding · *Vitis* · Genetic resources

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10.1 Introduction

Cultivated grapes are one of the most valuable and diverse horticultural crops in the world. As of 2013, grape production (for wine, fresh fruit, raisins, juice, and distilled products) accounted for over 5 billion dollars in annual revenue in the United States alone (USDA 2013). The most widely cultivated grape species, *Vitis vinifera* L., was domesticated in modern-day Northern Iran (Chataigner 1995; McGovern and Michel 1995; Zohary 1996; Zohary and Hopf 2000) between 6000 and 5000 BC during the Neolithic era (Amerine and Singleton 1977; Mullins et al. 1992; McGovern et al. 1996; McGovern 2013). *Vitis vinifera* was domesticated from its antecedent, *V. sylvestris*, which is now considered a subspecies of *V. vinifera* (Levadoux 1956; Mullins et al. 1992). Prior to domestication, wild *V. vinifera* ssp. *sylvestris* (C.C. Gmel) Hedi selections were found and collected along the banks of the Caspian and Black Seas (Zohary and Spiegel-Roy 1975; Ketsa and Verheij 1992) and in the region's semi-deciduous forests (Levadoux 1956; Arnold et al. 1998). The defining aspect of wild grapevine domestication was the selection of a hermaphroditic, rather than dioecious, mode of reproduction. This move to self-pollination in cultivated vines ensured high fruit set without the need for an external male (pollinator) vine. With the exception of rare mutations, cultivated *V. vinifera* is still unique among the near-universally dioecious wild *Vitis* species.

Following domestication, the Greeks and Phoenicians distributed cultivated vines as clonal cuttings across the rest of the Middle and Near East as well as Europe over the next few thousand years (Grassi et al. 2003; Arroyo-García et al. 2006). Distribution followed trade routes and the movement of civilizations, and during this period of expansion, the practice of grape growing and importance of wine became deeply integrated into various cultures and religions. Cortez introduced *V. vinifera* into the new world via Mexico about 1525 AD (Mullins et al. 1992). By the late 1600s, grape growing had spread across Latin America and north along the western coast of North America as Catholic missionaries cultivated grapes to supply sacramental wines (Mullins et al. 1992). During this time, European colonists were also introducing *V. vinifera* varieties from their home countries to the eastern coast of North America. Early plantings of *V. vinifera* vines in this area quickly died as a result of pests, diseases, and abiotic stress such as cold. The failure of *V. vinifera* caused the early settlers to look to the better-adapted wild grape species native to North America. This recognition eventually led to large-scale breeding efforts by the mid-nineteenth century to incorporate the pest and disease resistance of the American species with the high fruit and wine quality of the *V. vinifera*-derived varieties, resulting in a new class of grape cultivars called American hybrids in the United States and the hybrid direct producers in France.

Unfortunately, one of the unintended consequences of the movement of plant material between the New and Old World was the introduction of powdery (*Erysiphe necator* Schwein.) and downy mildew (*Plasmopara viticola* (Berk & Curt.) Berl. & de Toni) and the root pest phylloxera (*Daktulosphaira vitifoliae* Fitch) from North America into England in 1845 (Campbell 2006). The mildews and phylloxera

devastated the European grape and wine industry. In 1873, phylloxera was also detected in a Sonoma county, California vineyard (Bioletti et al. 1921; Campbell 2006). Rootstock breeding programs began in response to the phylloxera invasion of Europe, as a way to combine the desirable fruit characteristics of *V. vinifera* with the resistance to phylloxera in the roots of North American *Vitis* species. These programs evaluated multiple wild species from North America and quickly became focused on two species that were easy to root and propagate from dormant cuttings, *V. riparia* Michaux and *V. rupestris* Scheel (Viala and Ravaz 1903; Bioletti et al. 1921). Later, *V. berlandieri* Planchon was also integrated into rootstock breeding programs as a response to the need for lime tolerance (Viala and Ravaz 1903). Rootstock selection today still revolves primarily around *V. rupestris*, *V. riparia*, and *V. berlandieri* as pure species and in hybrid combinations.

Although it was widely assumed at the time that all native North American grapevine species would be equally resistant to phylloxera feeding, these initial rootstock breeding and establishment efforts soon discovered that some species were more resistant than others (Lider 1958). This prompted much of the initial evaluation work designed to classify the resistance and viticultural attributes of rootstocks by genetic parentage (Ramming 2010). The initial work on phylloxera resistance in California was supported by the State Viticulture Commission (Doyle 1894). This work resulted in the discovery that rootstock performance was greatly influenced by site, although a detailed classification of rootstock influence on scion attributes and characteristics was not thoroughly explored at that time.

A second era of rootstock and wild species evaluation began in California in the 1980s after the widely used but inadequately resistant rootstock AXR#1 (*V. vinifera* ‘Aramon’ x *V. rupestris* ‘Ganzin’) began failing to phylloxera (Granett et al. 1985, 1987). AXR#1’s failure was due to the *V. vinifera* parentage in its background and the existence and selection of phylloxera strains capable of feeding aggressively on its root system. Wine grape growers were forced to replant the damaged acreage and select from a range of different phylloxera-resistant rootstocks with very little current knowledge as to the impact any given rootstock would have on scion growth and development. Current rootstock breeding is shifting to a focus on rootstock-scion interactions and expanding beyond phylloxera resistance.

In addition to the continued threat of phylloxera and fungal pathogens, the global expansion of viticulture into diverse environments has resulted in additional pressures such as nematodes, Pierce’s disease (caused by an insect-vectored bacterium, *Xylella fastidiosa*; Wells et al. 1987), viruses and virus complexes, and the need for cold and drought tolerance. *Vitis vinifera*, though broadly adapted to conditions throughout Europe, does not carry tolerance or resistance to New World pests and diseases that have been spread throughout the world on plant material. For the industry to continue to thrive, new sources of resistance and mechanisms for tolerance must be identified and incorporated into both rootstock and scion breeding programs. Wild *Vitis* species from North America have coevolved with a broad range of pressures currently challenging the global viticulture industry and can continue to provide valuable traits for breeding. In addition to their value to the viticulture industry, many of these species have a long history of wild utilization by

indigenous groups and present opportunities for the production of industrial and medicinal compounds. North American *Vitis* species have very high value, and their conservation and utilization present an opportunity for crucial contributions to global agriculture.

10.2 Grapevine Wild Relatives in North America

North America is home to about 30 species of wild *Vitis*, and recent studies have suggested that it is the center of origin of the genus (Wan et al. 2013). These species are all dioecious, and with the exception of subgenus *Muscadinia* from the Southeastern United States, all of the species are interfertile. This missing reproductive barrier encourages species diversity and has helped *Vitis* species to inhabit a wide range of environments throughout the continent. However, it has also created a complicated scenario of closely related species and interspecific hybrids in areas where ranges overlap. Despite several species descriptions for *Vitis* (Munson 1909; Brizicky 1965; Moore 1991), a detailed phylogenetic reconstruction of the genus has not yet been published.

Most of the species richness is concentrated in the Eastern United States (Fig. 10.1), with high levels of diversity in central Texas. Legendary viticulturist T.V. Munson first documented the rich diversity of *Vitis* species in Texas in his 1909 treatise, “Foundations of American Grape Culture” (Munson 1909). The number of morphologically distinct species that occur together across Texas is unprecedented globally, perhaps with the exception of certain areas of China. Texas is also critical to the history of rootstock breeding, as it has the only grape habitat in North America with significant limestone deposits. Limestone soils dominate the viticultural regions of Europe, and the first generation of rootstocks bred from *V. rupestris* and *V. riparia* was incapable of growing well on those soils. French grape breeders contacted Munson for advice, and he suggested the use of *V. berlandieri* (now *Vitis cinerea* (Engelm. in Gray) Engelm. ex Millardet var. *helleri* (Bailey) M.O. Moore), a species endemic to the limestone hills of central Texas. This led to the hybridization of this species with *V. riparia* and *V. rupestris* and the development of most of the rootstocks used around the world (Campbell 2006). Texas is also home to the only known grape species to grow away from any apparent permanent water source, *V. monticola* Buckley, and two species of suspected hybrid origin: *V. X champinii* Planchon and *V. X doaniana* Munson ex Viala (Munson 1909; Pavek et al. 2003).

Historical and current breeding efforts have focused on a relatively small group of species – these are profiled in detail below as either “rootstock species” (Fig. 10.2) or “scion species” (Fig. 10.3), though some overlap these categories. The majority of North American *Vitis* species are either less utilized or less understood, however, and fall under a more traditional definition of “crop wild relatives.” They represent useful genetic diversity in traits of interest for breeding and could form the basis of future work but will only be introduced here in the interest of brevity (Table 10.1).

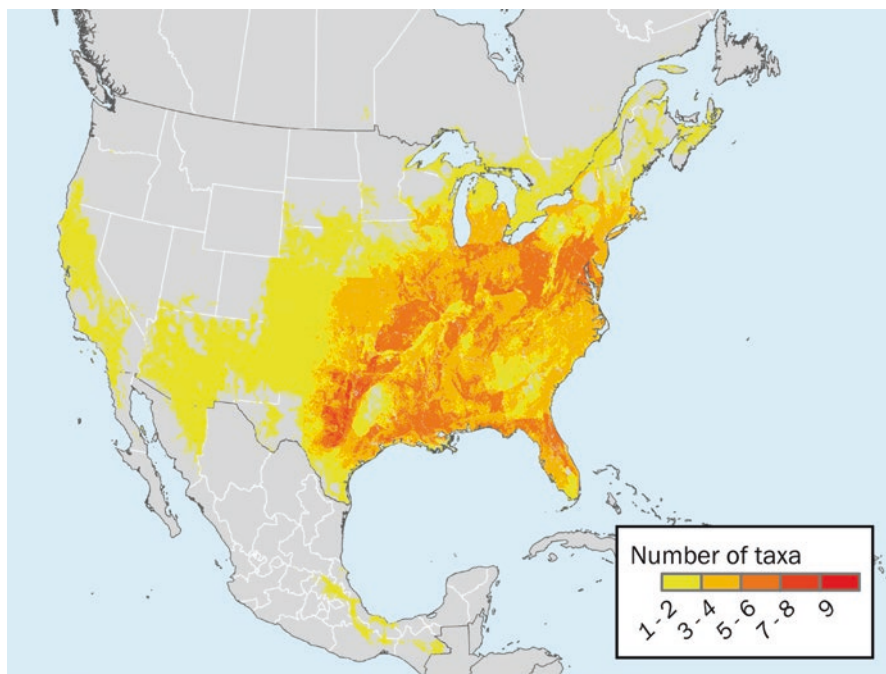


Fig. 10.1 Species richness map of modeled potential distributions of North American *Vitis*. The map displays overlapping potential distribution models for assessed taxa. Warmer colors indicate areas where greater numbers of taxa potentially occur in the same geographic localities. Full methods for generation of maps and occurrence data providers are listed in Appendix 1

10.2.1 Rootstock Species

Vitis riparia It typically grows in moist, fertile soils near bodies of water. Its broad range extends across most of eastern North America: from the Rocky Mountains to the Atlantic Ocean, from northern Texas, Mississippi, and Louisiana to Southern Canada, and from New Brunswick to Saskatchewan (Pongracz 1983; Moore 1991). This species was essential in reestablishing European vineyards after the importation of phylloxera (Viala and Ravaz 1903; Pongracz 1983), and still many of the most important rootstocks in use today are derived from *V. riparia*.

Beyond phylloxera resistance, *V. riparia* is associated with several viticulturally significant traits. For example, rootstocks with *V. riparia* parentage (i.e., “101–14 Mgt”) exhibit relatively early phenology compared with other *Vitis* species and are associated with early ripening of berries and early senescence (Dodson Peterson and Walker 2017). In addition, the low vigor associated with *V. riparia* is frequently exploited in choosing rootstocks for vineyard sites with deep, moist, fertile soil to restrict scion vigor and maintain high fruit quality.

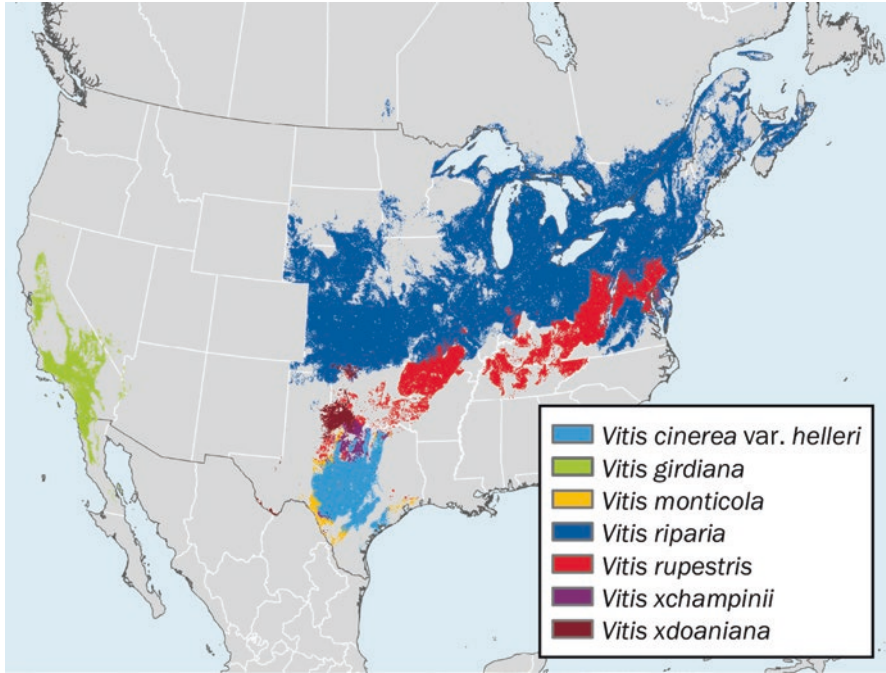


Fig. 10.2 Modeled potential distribution of *Vitis* species used in rootstock breeding: *V. riparia* Michx., *V. rupestris* Scheele, *V. cinerea* (Engelm.) Millardet var. *helleri* (L. H. Bailey) M. O. Moore, *Vitis xchampinii* Planch., *V. girdiana* Munson, *V. xdoaniana* Munson ex Viala, and *V. monticola* Buckley, based on climatic and edaphic similarities with herbarium and genebank reference localities. Full methods for generation of maps and occurrence data providers are listed in Appendix 1

The exceptional range of this species has resulted in a broad adaptation to various environmental conditions, particularly in temperature. In fact, Viala and Ravaz (1903) reported that specimens were found in regions with low temperatures reaching -30°C , an observation supported by the work of Pierquet and Stushnoff (1980), who tested the association of low temperature exotherms with the viability/death of primary and secondary buds in *V. riparia*. Most grape breeding programs focusing on developing scion cultivars for colder climates have utilized *V. riparia* in complex hybrids (Fisher 1980; Luby 1991), with newer cultivars developed at the University of Minnesota showing hardiness to almost -40°C (Hemstad and Luby 2000). Interestingly, *V. riparia* accessions from more southerly locations might exhibit better winter hardiness than those from northerly locations, due to reduced response to temperature fluctuations during winter (Londo and Martinson 2015).

While *V. riparia* is generally considered drought sensitive, there is limited evidence for adaptation to drier conditions in some forms the species. For instance, the dune grape (*V. riparia* var. *syrticola*) is restricted to the dunes along the Great Lakes shoreline in Southern Ontario and might be a germplasm source for combined cold and drought tolerance (Catling and Mitrow 2005; Rahemi et al. 2016).

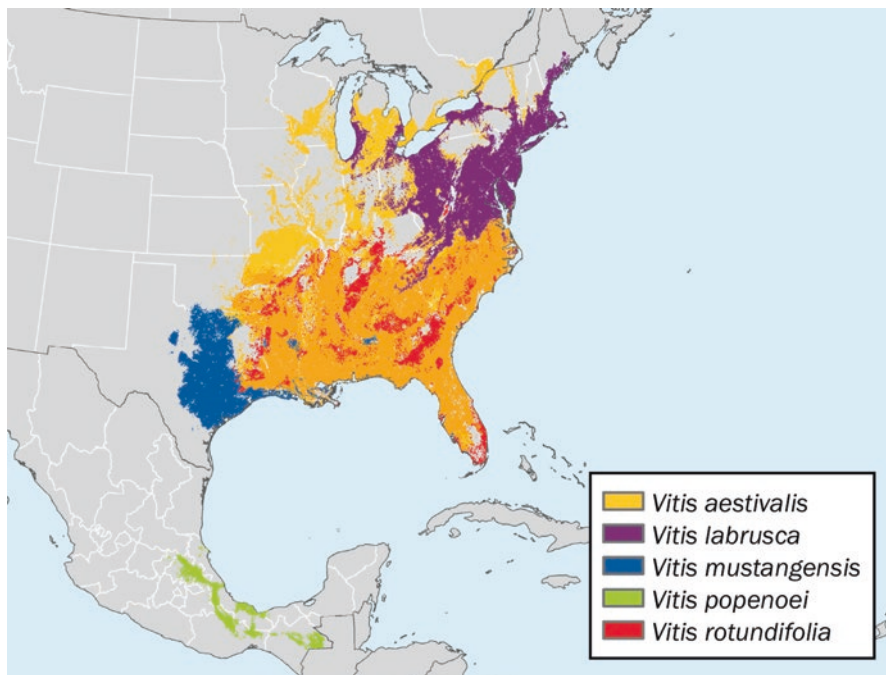


Fig. 10.3 Modeled potential distribution of *Vitis* species used in scion breeding: *V. aestivalis* Michx., *V. labrusca* L., *V. mustangensis* Buckley, *V. popenoei* J. H. Fennel, and *V. rotundifolia* Michx. based on climatic and edaphic similarities with herbarium and genebank reference localities. Full methods for generation of maps and occurrence data providers are listed in Appendix 1

Vitis riparia is one of several North American grape species resistant to the fungal disease downy mildew (*Plasmopara viticola*) (Alleweldt 1980; Alleweldt et al. 1990; Staudt and Kassemeyer 1995) and has been used in studies aimed at identifying quantitative trait loci (QTL) for downy mildew resistance (Marguerit et al. 2009). The species has also been cited as a potential source for resistance to fungal diseases including botrytis bunch rot (*Botrytis cinerea* Pers.), black rot (*Guignardia bidwellii* (Ellis) Viala & Ravaz), and powdery mildew (*Erysiphe necator*) (Alleweldt 1980; Alleweldt et al. 1990).

In 2015, USDA-ARS researchers reported the discovery of a novel polysaccharide in the stem exudate of *V. riparia* and named it Frost Grape Polysaccharide (FGP) (Price et al. 2015). FGP has potential for the food and cosmetic industries as an emulsifier similar to currently imported gum arabic but without the potential for allergy sensitization (Hay et al. 2017). More research is necessary to determine the exact properties and uses for this compound and whether or not it is produced in other related *Vitis* species (Leathers et al. 2017).

Vitis rupestris It has a low-growing, shrubby habit and is native to rocky streambeds. At one time it was abundant along a narrow band from southwestern Texas, through Oklahoma, Arkansas, Missouri, and continuing northeast to the Pennsylvania

Table 10.1 Introduction and key traits for select North American grape wild relatives

Species	Native area	Key traits and references
<i>V. acerifolia</i> Raf. Syn.: <i>V. longii</i> Prince, <i>V. solonis</i> Hort. Berol. ex Planchon	North-central Texas and Western Oklahoma, extending to parts of Kansas, Colorado, and New Mexico	Salt tolerance (Heintz 2016) Drought (Padgett-Johnson et al. 2003)
<i>V. arizonica</i> Engelm.	Arizona, New Mexico, north-central Mexico, extending into Texas	Drought tolerance (Padgett-Johnson et al. 2003; Knipfer et al. 2015) Pierce's Disease (<i>Xylella fastidiosa</i>) resistance (Riaz et al. 2006) Dagger nematode (<i>Xiphinema index</i> Thorne and Allen, 1950) resistance (Xu et al. 2008)
<i>V. californica</i> Bentham	Central and Northern California, extending into Oregon	Hybridization with cultivated <i>V. vinifera</i> (Dangl et al. 2015)
<i>V. cinerea</i> (Engelm. in Gray) Engelm. ex Millardet (excl. var. <i>helleri</i>)	Broadly through central and eastern Mexico and Southeastern United States, extending north to Pennsylvania	General fungal disease resistance genes (Mahanil et al. 2007) Tropical root-knot nematode (<i>Meloidogyne javanica</i> Treub, 1885) resistance (Smith et al. 2014) Strong phylloxera resistance (Zhang et al. 2009)
<i>V. shuttleworthii</i> House	Northern Florida, rare	Anthracnose (<i>Elsinoe ampelina</i> Shear) resistance (Mortensen 1981)
<i>V. treleasei</i> Munson ex L.H. Bailey	Arizona and New Mexico	Salt tolerance (Heintz 2016) Drought tolerance (Padgett-Johnson et al. 2003)
<i>V. vulpina</i> L. Syn.: <i>V. cordifolia</i> Michaux	Broadly in Eastern United States, south of the Great Lakes and New York, south to Texas, and east to the Atlantic	Cold tolerance (Luby 1991)

Ozarks – but the range is now much more restricted. By 1909, Munson noted that the populations of this species were shrinking due to grazing (Munson 1909). The current range is restricted to the Ozark Plateau in southern Missouri and northern Arkansas and a small number of isolated populations in Oklahoma and Texas (Moore 1991; Pap et al. 2015) (Fig. 10.4). The shrubby, non-climbing growth habit makes these vines particularly susceptible to grazing, though riparian habitat degradation is also a serious factor in the decline of this species (Moore 1991). Due to the increasing vulnerability of wild populations and the great historical and potential value of the species for the viticulture industry, four locations in Missouri and Oklahoma were established as the first NPGS in situ conservation sites for an American crop wild relative (Pavek et al. 2003).

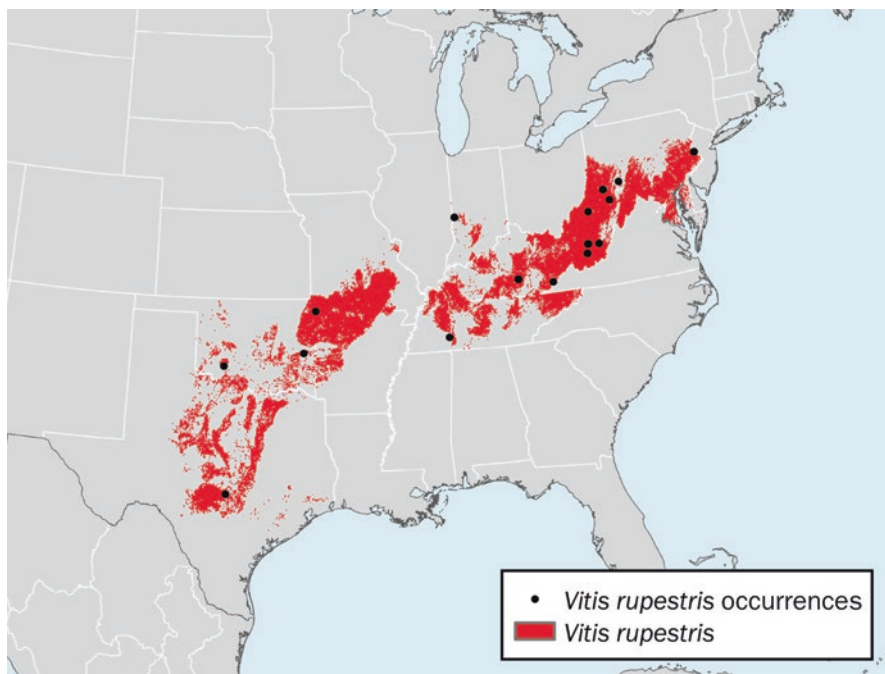


Fig. 10.4 Red shading indicates the modeled potential distribution of *V. rupestris* Scheele collections based on climatic and edaphic similarities with historic herbarium and genebank reference localities. Black circles indicate remaining occurrences of known wild populations. Full methods for generation of maps and occurrence data providers are listed in Appendix 1

Vitis rupestris was one of the first North American *Vitis* species utilized for grapevine breeding, initially as a source of downy mildew resistance and later, with *V. riparia*, as the foundation of the first phylloxera-resistant rootstocks (Viala and Ravaz 1903; Galet 1988; Di Gaspero et al. 2012). In addition to durable phylloxera resistance, the species possesses other important characteristics that are likely derived from its adaptation to nutrient-poor, gravelly soils (Pongracz 1983; Reisch et al. 2012). Rootstocks with *V. rupestris* parentage are effective at excluding chloride from the scion, an indication of salt tolerance (Sauer 1968; Tregeagle et al. 2006; Fort et al. 2015), and have a deep rooting profile (Morano and Kliewer 1994; Fort et al. 2017). *Vitis rupestris* is also still an important source of powdery mildew resistance (Barba et al. 2014).

Vitis cinerea var. *helleri* It has been extensively used in rootstock breeding. Originally named *V. berlandieri*, it is now considered to be a variety of *V. cinerea*. *Vitis cinerea* is a wide-ranging species, found throughout the Eastern United States south of the 40th parallel (Moore 1991), and *V. cinerea* var. *helleri* is restricted to central Texas and has been used extensively in grape rootstock breeding, due to its tolerance of limestone soils. This latter taxon was considered an independent species, *Vitis berlandieri* in early texts (Munson 1909; Bailey 1934; Galet 1988),

but Comeaux (1987) proposed reducing the species to a variety of *V. cinerea* based on field observations of intergradation between the two taxa. Despite possessing distinct characteristics in morphology, vigor, native habitat, and, crucially, lime tolerance (Viala and Ravaz 1903; Pongracz 1983; Schmid et al. 2009), the inclusion of *V. berlandieri* within *V. cinerea* has so far been supported by molecular evidence (Aradhya et al. 2013; Wan et al. 2013). Moore (1991) proposed the name ‘var. *helleri*’ for consistency with previous literature.

The small natural range of *V. cinerea* var. *helleri* is due to its adaption to the shallow, limestone-derived soils of the Edwards Plateau of central Texas southwest of the Brazos River and, sparsely, southwest toward the Rio Grande (Munson 1909; Hatch et al. 1990; Moore 1991). Although the region receives acute periods of precipitation, *V. cinerea* var. *helleri* is often found growing among dead or dormant grasses in dry soils (Morano and Walker 1995). Notably, much of the Edwards Plateau is historically rangeland, and the region holds one of the largest deer populations in North America (Hatch et al. 1990), suggesting that grazing has inhibited the proliferation of *V. cinerea* var. *helleri*.

Vitis cinerea var. *helleri* is remarkable for the narrowness of its ecological niche. Although the Edwards Plateau is a severe environment characterized partly by erratic precipitation, environmental factors including mean annual precipitation, seasonal temperature, and soil attributes are relatively uniform across the range of *V. cinerea* var. *helleri* (Hijmans et al. 2005; Hengl et al. 2017). The region, particularly the Hill Country west of Austin and north of San Antonio, is undergoing rapid residential and commercial development threatening the survival of this vital species. For this reason, ex situ conservation efforts might be most appropriate for maintaining *V. cinerea* var. *helleri* germplasm.

The lime-tolerant *V. cinerea* var. *helleri* was incorporated into rootstock breeding in the late 1800s when scions grafted to *V. riparia*- and *V. rupestris*-based rootstocks expressed lime-induced iron chlorosis on the limestone-derived soil common in the viticultural regions of Europe (Pongracz 1983). Because *V. cinerea* var. *helleri* is difficult to propagate, commercially viable rootstock cultivars utilizing this species are selected from crosses with *V. riparia* and *V. rupestris*. Other traits associated with *V. cinerea* var. *helleri*-based rootstocks, particularly hybrids with *V. rupestris*, include increased scion vigor, delayed phenology and senescence, drought resistance, and, in some instances, salinity tolerance. There is also evidence for reduced potassium uptake and/or transport in *V. cinerea* var. *helleri*-based rootstocks compared with other rootstocks in high-potassium soils (Rühl 1991, 1992; Wolpert et al. 2005).

Vitis xchampinii It is usually described as a natural hybrid between *V. mustangensis* Buckley x *V. rupestris*; however, there is disagreement among authors regarding its origin, which might also include hybridization with *V. cinerea* var. *helleri* and *V. monticola* Buckley. *Vitis X champinii* has been utilized in rootstock breeding, most notably for the cultivars ‘Ramsey,’ ‘Dog Ridge,’ ‘Harmony,’ and ‘Freedom.’ The species has also been used in developing fruit-bearing varieties such as the *V. X champinii* x *V. labrusca* L. hybrid ‘Champanel’ (Munson 1909). While associated with the Edwards Plateau in south-central Texas (Munson 1909; Moore 1991), the species

has become very rare in natural settings, and herbarium samples of this taxon were mostly deposited prior to 1900 (Comeaux 1987). The rapid development of the Texas Hill Country, intense herbivory from deer and cattle populations, and diminishing range of *V. rupestris* make the continued existence of this important species precarious, except in ex situ germplasm collections.

Both climate change and expansion of viticultural regions are causing the viticulture industry to look toward rootstock-scion combinations that tolerate or avoid drought and marginal soils. Recently, rootstock breeders have been developing interest in species native to arid regions of the Southwestern United States and Mexico for salt and drought tolerance (Heinitz et al. 2015). In this region, wild *Vitis* are restricted to isolated mountain ranges and riparian corridors. Seeds are dispersed primarily by birds and small mammals, and vines propagate vegetatively by layering during seasonal flooding, allowing gene flow between otherwise isolated habitats. Unfortunately grazing, drought, invasive species in riparian zones, and herbicide use along highways threaten much of the prime *Vitis* habitat in the Southwest.

Vitis girdiana Munson and *V. X doaniana* Munson ex Viala both performed well in initial screens for chloride exclusion (a measure of salt tolerance) (Heinitz 2016) and drought tolerance (Padgett-Johnson et al. 2003). *Vitis girdiana* is native to Southern California, Baja (Mexico), and Southern Nevada and has been observed in Southwest Utah (Wada 2008). It displays high vigor and growth rate even under high temperatures in its native habitat and remains prevalent in the landscape, though it is under threat of genetic erosion from hybridization with cultivated *V. vinifera* (Dangl et al. 2015). *Vitis X doaniana* is a well-accepted hybrid of *V. mustangensis* and *V. acerifolia* Raf., which occurs in a narrow region where the parent species co-occur near the Red River at the border of Texas and Oklahoma (Munson 1909; Moore 1991; Peros et al. 2011). Although this hybrid species has unique characteristics and great potential for breeding, it is not well represented in ex situ collections, and native populations are under threat from drought and land use change on both sides of the Red River. *Vitis monticola* is another unique species with a restricted natural range. Found exclusively in well-drained, upland sites in the Edwards Plateau in central Texas, the slow-growing *V. monticola* is among the grape species with the narrowest range (Moore 1991). Unlike nearly all other *Vitis* species that are associated with either seasonal or permanent water, *V. monticola* is frequently found growing without obvious water sources. This makes it a potentially important genetic resource for drought tolerance, but difficulty of propagation from woody cuttings and very slow growth are drawbacks in using this unique species in breeding programs.

10.2.2 Scion Species

Vitis aestivalis Michaux It is found on well-drained sites throughout the Eastern United States and Southern Canada (Munson 1909; Moore 1991). The species is composed of three subspecies (vars. *aestivalis*, *bicolor* Deam, and *lincecumii*

(Buckley) Munson) that were variously designated in early texts (Munson 1909; Bailey 1934; Galet 1988; Moore 1991). The original form identified as *V. aestivalis*, now designated var. *aestivalis*, is found in the Southeastern United States, from eastern Texas, north to southern Iowa, east to the Atlantic Coastal Plain, and south to Florida (Munson 1909; Moore 1991). The subspecies *bicolor* comprises the northern range of *V. aestivalis* but is also found in northern Alabama and Georgia (Munson 1909; Moore 1991). Finally, *V. aestivalis* var. *lincecumii* (the Post Oak Grape) is mostly restricted to East Texas and Western Louisiana (Munson 1909; Moore 1991).

Historically, *V. aestivalis* was important in developing the French-American hybrids, with *V. aestivalis* var. *lincecumii* playing a central role in complex hybrids among American species and *V. vinifera* (Reisch et al. 1993; Robinson et al. 2012). Indeed, Munson (1909) utilized this subspecies extensively in his breeding efforts, and it might be useful as a source of heat tolerance in modern breeding efforts (Reisch and Pratt 1996). *Vitis aestivalis* accessions show partial resistance to downy mildew (Staudt and Kassemeyer 1995; Cadle-Davidson 2008), and the early American cultivar ‘Norton,’ likely a *V. aestivalis* x *V. vinifera* hybrid (Stover et al. 2009), is resistant to powdery mildew (Fung et al. 2008). Although several French-American hybrids derived from *V. aestivalis* show disease resistance, the complex parentage of those cultivars makes associations among traits, alleles, and species difficult (Dalbó et al. 2001; Fischer et al. 2004), further bolstering the need for conservation based on adaptive, phenotypic, and genetic diversity, as opposed to conservation based on taxonomy. Currently, *V. aestivalis* and hybrids with *V. aestivalis* parentage are used in breeding programs for eastern and northern climates, particularly in the Cornell program at Geneva (Reisch et al. 1993).

Vitis labrusca It is a vigorous vine that grows in a wide variety of wet habitats from Maine, New Hampshire, and Vermont to northern Georgia, Alabama, west to Mississippi, and north to Eastern Illinois and Southern Michigan (Munson 1909; Moore 1991). The species produces relatively large berries, which probably attracted human foragers and those attempting to improve North American grapes by selection and hybridization with European cultivars.

Early cultivars derived from *V. labrusca*, frequently from *V. labrusca* x *V. vinifera* hybrids but also from hybrids between *V. labrusca* and other North American species, were introduced in the first half of the nineteenth century (Hedrick et al. 1908; Munson 1909). The most well-known of these is ‘Concord,’ a seedling derived from a cross between *V. labrusca* and ‘Catawba,’ an early American hybrid with *V. labrusca* x *V. vinifera* parentage (Huber et al. 2016). Introduced in 1854, ‘Concord’ remains important for producing grape juice and preserves, with utilized US production exceeding 360,000 t in 2015 (USDA 2016).

Vitis labrusca was utilized in some early French-American hybrid wine grape cultivars of the early twentieth century (Robinson et al. 2012); however, the species was often avoided in crosses because of its undesirable “foxy” flavor (Reisch et al. 1993).

For this reason, cultivars with *V. labrusca* parentage are mainly utilized for juice and preserves, and several breeding programs utilize the species for table grape development (Clark and Moore 2015). Traits for which *V. labrusca* might serve as valuable germplasm include resistance to the fungal diseases powdery and downy mildew (Pearson and Goheen 1988; Alleweldt et al. 1990) and anthracnose (Mortensen 1981) and the phytoplasma disease Flavescence dorée (Pearson and Goheen 1988).

Subgenus *Muscadinia* The genus *Vitis* is currently divided into two subgenera: *Vitis* ($2n = 38$) and *Muscadinia* ($2n = 40$). The mostly subtropical *Muscadinia*, or muscadine grape, is comprised of *V. rotundifolia* Michaux and *V. popenoei* J.H. Fennel, with *V. rotundifolia* further divided into var. *rotundifolia* (found from Texas to Virginia and south to Florida), var. *munsoniana* (J.H. Simpson ex Planch.) M.O. Moore (found throughout Florida and in southern Georgia and Alabama), and var. *pygmaea* McFarlin ex D.B. Ward (found only in Central Florida) (Comeaux 1984; Moore 1991; Aradhya et al. 2013). The distribution of *V. popenoei* is limited to southern Mexico (Aradhya et al. 2013). Fossil (Kirchheimer 1939; Tiffney and Barghoorn 1976) and molecular evidence (Trondle et al. 2010; Aradhya et al. 2013) indicate that the two subgenera once occupied similar ranges before diverging during the Tertiary period which lasted from ~66 million to 2.6 million years ago. Restriction of *Muscadinia* to the Southeastern United States and Mexico probably occurred during periods of glaciation.

The muscadine grape is historically important in the southern United States, where it has been used for wine, preserves, and table fruit (Olien 1990). The ‘Scuppernong’ grape is the best-known *V. rotundifolia* cultivar and was thought to be planted in the mid-1500s in Sir Walter Raleigh’s colony (Hedrick et al. 1908; Munson 1909). While muscadine grapes have been cultivated since then, the vine that became the cultivar ‘Scuppernong’ was probably discovered in Northeastern North Carolina by Isaac Alexander about 200 years later in the mid-eighteenth century (Reimer 1909). Significant efforts to develop improved muscadine and muscadine x *vinifera* hybrids have been documented since the early twentieth century (Munson 1909; Reimer 1909; Dearing 1917), and public muscadine breeding programs continue in the United States, including at the University of Arkansas (Clark and Barchenger 2014), Georgia State University (Conner 2010), and North Carolina State University (NC State Extension 2016). In 2006, muscadine grapes were produced on approximately 2000 ha (5000 acres) in 12 states, with production trending upward (Cline and Fisk 2006).

Vitis rotundifolia is an important potential germplasm source for a range of disease, insect, and nematode resistance absent in *V. vinifera* (Alleweldt et al. 1990; Olien 1990; Staudt and Kassemeyer 1995), but chromosomal differences between the two subgenera make hybridization difficult. Although some *V. vinifera* x *V. rotundifolia* combinations exist (Patel and Olmo 1955; Dunstan 1962; Jelenkovic and Olmo 1968; Bouquet 1980), successful pollination is difficult to predict, and most F₁ populations are mostly or entirely sterile. Embryo rescue techniques have been used to improve progeny yields after attempted hybridization (Lu et al. 2000), and colchicine

has been used to induce tetraploidy in *V. vinifera* x *V. rotundifolia* hybrids for improved fertility in F₁ populations (Xie et al. 2015).

Jelenkovic and Olmo (1968) developed a partially fertile *V. vinifera* x *V. rotundifolia* population that exhibited tolerance to several important insects and diseases and was used in backcrosses to *V. vinifera* to develop new wine grape cultivars (Olmo 1971). *Vitis rotundifolia* has also been used in breeding programs for developing rootstocks resistant to dagger nematode (*Xiphinema index*) and, by extension, grapevine fanleaf virus, which is vectored by the nematode (Walker et al. 1991; Walker and Jin 2000; Esmenjaud and Bouquet 2009). Genes for powdery mildew resistance have been identified in *V. rotundifolia* and *V. vinifera* x *V. rotundifolia* populations (Pauquet et al. 2001; Riaz et al. 2011; Blanc et al. 2012), as well as downy mildew resistance (Merdinoglu et al. 2003).

Vitis mustangensis The mustang grape, *Vitis mustangensis* (syn. *V. candicans* Engelm. ex Gray), is the dominant grapevine taxon in eastern Texas, with an overall range that includes Western Louisiana and Southern Oklahoma, as well as a disjunct population in Alabama (Munson 1909; Moore 1991). The species is very vigorous and is often observed completely enshrouding and smothering trees and other structures. Although *V. mustangensis* has played only a limited and indirect role in global viticulture (rootstocks like ‘Ramsey’ and ‘Dog Ridge’ are selections of *V. X champinii*, a natural hybrid between *V. mustangensis* x *V. rupestris*), mustang wine is of local historical importance in Texas, and the species might be valuable in scion and fruit breeding. *Vitis mustangensis* inhabits common ranges with most other wild grapes in Texas, including the lime-tolerant *V. cinerea* var. *helleri* and the drought-resistant *V. monticola*, and therefore might act as a bridge among taxa and a source for genetic and phenotypic variation in other important taxa. Its utility in rootstock breeding is limited due to poor rooting from woody cuttings and excessive vigor.

10.3 Wild and Alternative Utilization of North American *Vitis* L.

Efforts to study and conserve wild grapevines are typically focused on assisting breeding programs for commercial viticulture. However, researchers in Mexico are investigating ways to continue the long tradition of direct utilization of wild grapevines, where there is great potential in the agricultural, pharmaceutical, and food industries (Franco-Mora and Cruz-Castillo 2012).

Historically, indigenous groups in central Mexico used wild grapevine stems as thread to build fishing nets, baskets, and fences (Franco-Mora and Cruz-Castillo 2012). Wild grapevines have been highly important in traditional medicine, where the fruit, leaf, root, and sap are used to prepare teas and infusions (Jiménez-Martínez et al. 2013). Historically, wild grapevines were used as a natural remedy to treat heart disease, gout, and inflammatory arthritis (Jiménez-Martínez et al. 2013).

Culturally, wild grapevines have a strong presence in Mexican cuisine. Flowers and fresh berries were used in regional dishes from the State of Mexico (Luna-Gaona et al. 2010; Sabas-Chavez et al. 2016). *Vitis tiliifolia* Humb. & Bonpl. ex Schult. has been used to produce wine in the state of Guerrero, and the states of Puebla and Mexico are producing grape liquor (Franco-Mora and Cruz-Castillo 2012). This species is also being used to produce jelly and optimized for sugar and phenolic compound content in the wild grapevine berries (Franco-Mora and Cruz-Castillo 2012).

Currently, wild grapevines are getting special attention for their potential as sources of antioxidants and fatty acids. Tobar-Reyes and collaborators (2009) are studying the presence of antioxidant compounds in wild grapevine leaves. Trans-resveratrol, a polyphenol that confers important health characteristics in wine, has been reported to be synthesized in wild *Vitis* leaves either wounded or infected by *Botrytis cinerea* Pers. Resveratrol has shown potential as an inhibitor in the development of cancer cells in vitro and in vivo (Jang et al. 1997; Alkhalaf 2007; Tobar-Reyes et al. 2009). Moreover, consumption of resveratrol has shown anti-inflammatory, antioxidant, and antifungal properties as well as preventative action against heart disease (Stein et al. 1999). Resveratrol content varies between accessions of wild grapes and is heavily affected by the environment (Tobar-Reyes et al. 2009; Franco-Mora and Cruz-Castillo 2012). It has been suggested that resveratrol might be the active ingredient in *Vitis* that makes it important in traditional medicine (Tobar-Reyes et al. 2009).

Vitis vinifera seeds contain up to 14% oil. This oil is already used in Italy, Spain, and France for culinary purposes due to its high smoke point. This oil can also be used in the cosmetic industry due to its moisturizing properties (Franco-Mora et al. 2015). Franco-Mora and collaborators (2015) determined that wild grapevine seeds also have significant oil content. The average percentage of oil in the seed was 16.7%, of which 71.5% was linoleic acid, 17.2% was oleic acid, 6.6% was palmitic acid, and 4.3% was stearic acid.

10.4 Conservation Status and Future Concerns

10.4.1 *In Situ* Conservation

Conservation of wild plants in their native habitats (in situ conservation) is beneficial in many ways – populations can continue to adapt in place to changing environmental stresses, unique hybrid forms can be maintained by continued gene flow between parent species, and large population sizes can be maintained at relatively low expense. However, in situ conservation requires the cooperation of landholders and sufficiently robust wild populations. Most wild *Vitis* species in the Eastern United States still maintain large populations over broad ranges, and specific conservation measures are not necessary. In some areas, wild grapevines are so prevalent that they are often considered nuisance plants, and the state of Ohio has designated all *Vitis* as a prohibited noxious weed when not maintained or controlled for 2 years (Ohio Admin. Code 901:5-37-01).

Unfortunately, many other species, particularly in the more arid Western United States, are becoming rarer in the wild. Grazing, development, and riparian habitat degradation through reduced water flow and invasion of non-native species all threaten grape wild relatives in certain areas. This is most evident in the case of *V. rupestris*, an important rootstock species which was once prevalent but now considered endangered in Indiana (Division of Nature Preserves 2002) and Pennsylvania (Thompson 1997), threatened in Kentucky (Kentucky State Nature Preserves Commission 2000), and of special concern in Tennessee (Tennessee Natural Heritage Program 2002). Other species currently on state concern lists are the following: *V. aestivalis*, endangered, Maine (Maine Natural Areas Program 1999); *V. cinerea* var. *baileyana* (Munson) Comeaux, endangered, Pennsylvania (Thompson 1997); *V. labrusca*, special concern, Kentucky (Kentucky State Nature Preserves Commission 2000); *V. X novae-angliae* Fernald (pro sp.) [*labrusca* x *riparia*], endangered, Pennsylvania (Thompson 1997) and Maryland (Maryland Natural Heritage Program 1997), and special concern, Connecticut (Connecticut Department of Environmental Protection 1998); *V. palmata* Vahl, rare, Indiana (Division of Nature Preserves 2002); and *V. vulpina*, endangered, New York (Department of Environmental Conservation 2000), and threatened, Michigan (Michigan Natural Features Inventory 1999).

Scientists in the USDA-ARS National Plant Germplasm System (NPGS) conducted a study in the late 1990s to determine appropriate in situ conservation sites for three *Vitis* species: *V. rupestris*, *V. shuttleworthii*, and *V. monticola* (Pavek et al. 2000). They negotiated agreements with the landholders for four of seven sites identified for *V. rupestris* in Oklahoma and Missouri (Pavek et al. 2003) and tentative agreements with public land administrators at four Florida sites for *V. shuttleworthii* and three Texas sites for *V. monticola* (Pavek et al. 2000). At the time, these were the first official in situ conservation sites to be added to the NPGS system for any crop wild relative, and they were intended to complement but not replace the ex situ collections.

10.4.2 Ex Situ Conservation

Maintaining viable collections of seed or clonal plant material (ex situ conservation) can help ensure the safety of wild plants that are threatened in their natural habitats and allows for rapid access to diverse germplasm. Though ex situ conservation of clonal plants is expensive, it does allow for specific wild accessions to be preserved and propagated indefinitely. Also, the high level of heterozygosity in *Vitis* means that it is possible to capture a greater amount of allelic diversity with fewer individual plants.

Though global grape genebank collections are comprised mainly of cultivated *V. vinifera* varieties, most contain at least a small number of North American *Vitis* species due to their important history in rootstock breeding. The Vassal-Montpellier Grapevine Biological Resources Center, hosted by the French National Institute for Agricultural Research (INRA), has maintained collections from the original French breeders of the first grape rootstocks in the mid-nineteenth century. The University

of California, Davis Viticulture and Enology Department (UC Davis V&E), also maintains a large collection of North American *Vitis* for rootstock and scion breeding that has been collected over the last 30 years. The most accessible wild *Vitis* collection is maintained by the NPGS in the United States, both at the National Clonal Germplasm Repository in Davis, California (NCGR-Davis), and the Plant Germplasm Resources Unit in Geneva, New York (Aradhya et al. 2013). The number of accessions of various species in the NPGS collection and their availability for distribution is summarized in Fig. 10.5. While some species are well represented,

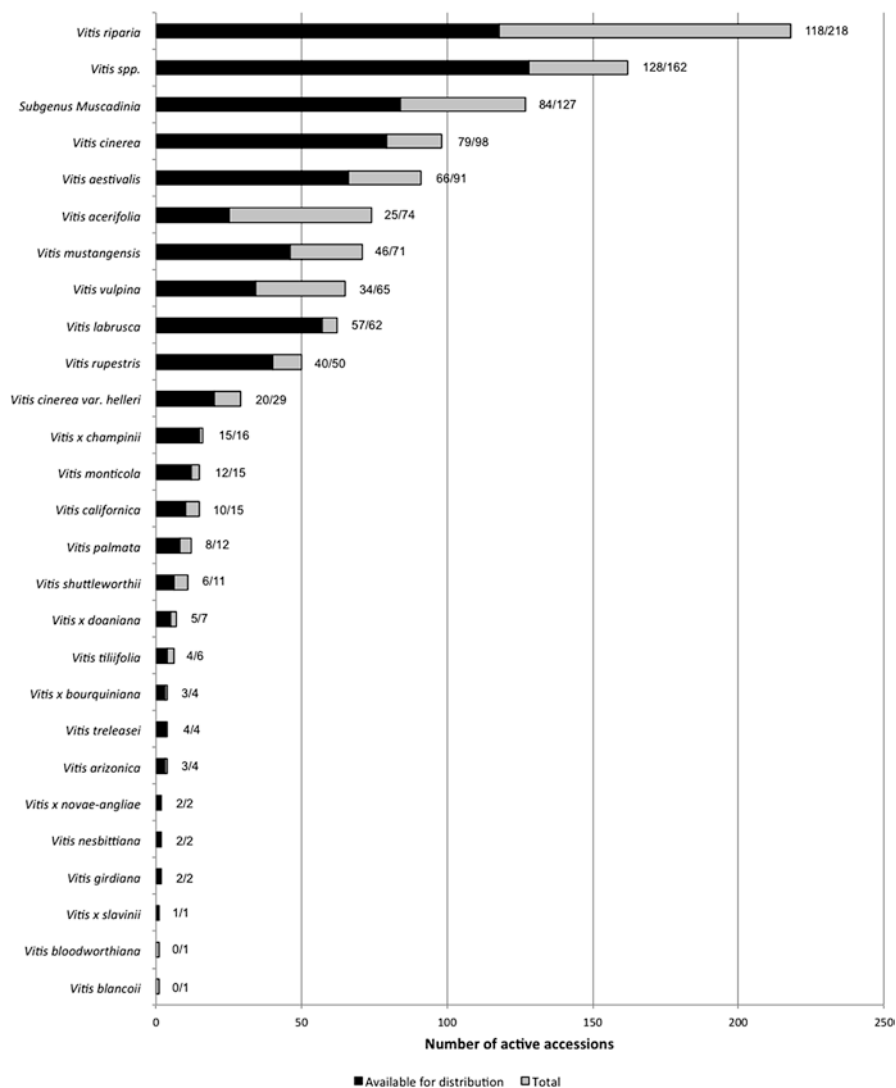


Fig. 10.5 Active accessions of North American *Vitis* in the National Plant Germplasm System (NPGS). Values are (number available for distribution)/(total number of accessions)

the lack of diversity in others such as *V. arizonica* and *V. girdiana* means that these species are often underrepresented in phylogenetic studies and other characterization efforts which rely on publicly available germplasm (e.g., Trondle et al. 2010; Peros et al. 2011). The addition of more diversity from the UC Davis V&E collection would help remedy this problem, but additional accessions cannot currently be added due to restricted field space and resources at NCGR-Davis.

10.4.3 Future Efforts

Characterization and utilization are key to the continued conservation of grape wild relatives in North America. More knowledge of the complex genetic relationships between species and unique populations of wild *Vitis* will allow for informed efforts at both ex situ and in situ conservation. Characterization of potentially useful traits will encourage utilization and can eventually lead to improved rootstock and scion varieties for a viticulture industry that is dealing with increasing environmental challenges.

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