Chapter 9
North American Crop Wild Relatives of Temperate Berries (*Fragaria* L., *Ribes* L., *Rubus* L., and *Vaccinium* L.)

Kim E. Hummer, Karen A. Williams, and Jill M. Bushakra

Abstract The crop wild relatives of temperate berry species abound on the North American continent, where more than 180 species are endemic. The development and production of berry crops, such as strawberries (*Fragaria* L.), currants and gooseberries (*Ribes* L.), raspberries and blackberries (*Rubus* L.), and blueberries and cranberries (*Vaccinium* L.), have global economic importance. The cultivated crops derived from these species have a total global annual farm gate value of roughly USD $3.7 billion, with production on the rise. Global strawberry production is more than twice the combined production of other temperate berry crops. Berries are highly nutritious and positively impact consumer health and vitality. Significant North American genetic resources have contributed to the development and cultivation of these globally produced and consumed crops.

Keywords Germplasm · Genetic resources · Small fruit · Soft fruit · *Fragaria* · *Ribes* · *Rubus* · *Vaccinium* · Strawberries · Currants · Gooseberries · Raspberries · Blackberries · Blueberries · Cranberries

9.1 Introduction

The North American landscape is rich with endemic species that are crop wild relatives (CWR) of the berry crops of *Fragaria*, *Ribes*, *Rubus*, and *Vaccinium*. Compared to grain crops that have been cultivated for millennia, temperate berry crops are much younger; selection, development, and domestication of the berries

---

K. E. Hummer (✉) · J. M. Bushakra
USDA, Agricultural Research Service,
National Clonal Germplasm Repository, Corvallis, OR, USA
e-mail: kim.hummer@ars.usda.gov; jill.bushakra@ars.usda.gov

K. A. Williams
USDA, Agricultural Research Service, Beltsville Agricultural Research Center,
National Germplasm Resources Laboratory, Beltsville, MD, USA
e-mail: karen.williams@ars.usda.gov

S. L. Greene et al. (eds.), *North American Crop Wild Relatives, Volume 2*,
https://doi.org/10.1007/978-3-319-97121-6_9

began between 100 and 750 years ago, depending on the crop. More than 180 species are endemic to North America (Table 9.1). The primary, secondary, and tertiary gene pools of the berry species were delineated by Wiersema and León (2016) and are presented (Table 9.1). Maps of the geographic distribution of the North American berry taxa are provided.

9.2 Strawberries (*Fragaria* L.)

9.2.1 Origin and Brief History of Use

The genus *Fragaria* is a member of the rose family (Rosaceae) and includes 22 species worldwide (Liston et al. 2014), although some subspecific designations remain unresolved at the molecular level (Hokanson et al. 2006). The cultivated strawberry of present-day commerce, *Fragaria* × *ananassa*, has a North and South American origin and is recent for a globally cultivated economically important crop. Its hybrid origin is specifically documented between 1714 and 1759 (Staudt 1962). Antoine Duchesne (1766) was first to observe the accidental hybrid and name this species. The mother of the large-fruited strawberry was a white-fruited South American landrace of *F. chiloensis* (L.) Mill. subsp. *chiloensis* f. *chiloensis*, and the pollen parent was the small, red-fruited North American *F. virginiana* Mill. subsp. *virginiana*. The original pollen parent was likely brought to France from the St. Lawrence River Basin, either from Quebec or Nova Scotia, Canada, by either Samuel Champlain or Louis Hébert in the early 1600s (Desjardins, personal communication, 2016). Thus, it had been "waiting" in Europe for over 100 years before the arrival of the South American landrace. Both of these American strawberry species and the resulting accidental hybrid offspring are octoploid.

9.2.2 Modern-Day Use and Agricultural Importance

In 2014, about 8,114,373 MT of strawberries were produced in about 78 countries (UNFAO 2017). In 2014, the US strawberry crop of about 1.36 billion MT was valued at $2.9 billion, with the fresh market value comprising about 81% (value $2.6 billion) and the remainder (value $241.8 million) used for processing (USDA-NASS 2015). California leads the USA in strawberry production with about 68% of the acreage, followed by Florida (USDA-NASS 2015). However, because strawberries are highly perishable, they are grown widely throughout the USA. Strawberries rank as the fifth most popular fresh market fruit in the USA, with per capita consumption increasing steadily to 3 kg per year in 2010 (USDA-ERS 2010). The USA is followed by the other major producing countries of Spain, Turkey, Mexico, Egypt, Russian Federation, Japan, Republic of Korea, and Poland (UNFAO 2017).

Table 9.1 Taxa and ex situ conservation of temperate berry crop wild relatives

Genus	Taxon	Ploidy	Gene pool	Number of accessions in NPGS[a]	Number of accessions in PGRC (Canada)[b]	Number of accessions in BGCI[c]	Number of accessions in GENESYS[d]
Fragaria L.	*Fragaria cascadensis* K. E. Hummer	10	2	52		2	33
Fragaria L.	*Fragaria chiloensis* (L.) Mill.	8	1	18	829	43	169
Fragaria L.	*Fragaria chiloensis* (L.) Mill. subsp. *chiloensis* f. *chiloensis*	8	1	22			23
Fragaria L.	*Fragaria chiloensis* (L.) Mill. subsp. *chiloensis* f. *patagonica* Staudt	8	1	283			276
Fragaria L.	*Fragaria chiloensis* (L.) Mill. subsp. *lucida* (E. Vilm. ex Gay) Staudt	8	1	26			20
Fragaria L.	*Fragaria chiloensis* (L.) Mill. subsp. *pacifica* Staudt	8	1	38			35
Fragaria L.	*Fragaria chiloensis* L. subsp. *sandwicensis* (Decne.) Staudt	8	1	2			2
Fragaria L.	*Fragaria mexicana* Schltdl. (=*Fragaria vesca* f. *bracteata* (A. Heller) Staudt)	2	3			1	
Fragaria L.	*Fragaria vesca* L. subsp. *bracteata* (A. Heller) Staudt	2	3	75			58
Fragaria L.	*Fragaria vesca* L. subsp. *americana* (Porter) Staudt	2	3	15			18
Fragaria L.	*Fragaria vesca* L. f. *bracteata* (A. Heller) Staudt	2	3	2		1	58
Fragaria L.	*Fragaria vesca* L. subsp. *californica* (Cham. & Schltdl.) Staudt	2	3	11		5	10
Fragaria L.	*Fragaria virginiana* Mill.	8	1	246	186	58	376
Fragaria L.	*Fragaria virginiana* Mill. subsp. *glauca* (S. Watson) Staudt	8	1	56			52
Fragaria L.	*Fragaria virginiana* Mill. subsp. *grayana* (Vilm. ex J. Gay) Staudt	8	1	50			50
Fragaria L.	*Fragaria virginiana* Mill. subsp. *platypetala* (Rydb.) Staudt	8	1	26		6	49
Fragaria L.	*Fragaria virginiana* Mill. subsp. *virginiana*	8	1	62			58
Fragaria L.	*Fragaria* × *ananassa* Duchesne ex Rozier (cultivated)	8	1	575	781	24	1552
Fragaria L.	*Fragaria* × *ananassa* Duchesne ex Rozier nothosubsp. *ananassa*	8	1	1			
Fragaria L.	*Fragaria* × *ananassa* Duchesne ex Rozier nothosubsp. *cuneifolia*	8	1	58		6	21
Fragaria L.	*Fragaria* × *bringhurstii* Staudt	4, 5, 6, 9	2	16		1	16
Ribes L.	*Ribes acerifolium* Howell	2	3	3		1	3

(continued)

Table 9.1 (continued)

Genus	Taxon	Ploidy	Gene pool	Number of accessions in NPGS[a]	Number of accessions in PGRC (Canada)[b]	Number of accessions in BGCI[c]	Number of accessions in GENESYS[d]
Ribes L.	*Ribes affine* Kunth	2	3			2	
Ribes L.	*Ribes amarum* McClatchie	2	3	2		10	2
Ribes L.	*Ribes americanum* Mill.	2	2	9		61	12
Ribes L.	*Ribes aureum* Pursh	8	2	48	7	128	68
Ribes L.	*Ribes binominatum* A. Heller	2	1	3		1	3
Ribes L.	*Ribes bracteosum* Douglas	2	1	25		25	30
Ribes L.	*Ribes californicum* Hook. & Arn.	2	2			5	
Ribes L.	*Ribes californicum* var. *hesperium* (McClatchie) Jeps.	2	2	1		3	1
Ribes L.	*Ribes cereum* Douglas	2	2	32		28	54
Ribes L.	*Ribes cereum* Douglas var. *inebrians* (Lindl.) C. L. Hitchc. (=*Ribes cereum* var. *cereum*)	2	2			1	
Ribes L.	*Ribes cereum* Douglas var. *cereum*	2	2	1		4	3
Ribes L.	*Ribes cereum* Douglas var. *colubrinum* C. L. Hitchc.	2	2	2		1	1
Ribes L.	*Ribes ciliatum* Humb. & Bonpl. ex Willd.	2	2	1		2	2
Ribes L.	*Ribes coloradense* Coville (=*Ribes laxiflorum* Pursh)	2	2			1	
Ribes L.	*Ribes cruentum* Greene (=*Ribes roezlii* var. *cruentum* (Greene) Rehder)	4	2	1		3	4
Ribes L.	*Ribes curvatum* Small	2	2	3		2	3
Ribes L.	*Ribes cynosbati* L.	2	1	7		32	13
Ribes L.	*Ribes diacanthum* Pall.	4	2	3		35	6
Ribes L.	*Ribes divaricatum* Douglas	6	2	1	1	53	7
Ribes L.	*Ribes echinellum* (Coville) Rehder	2	3	3		8	3
Ribes L.	*Ribes erythrocarpum* Coville & Leiberg	2	3	4		2	19
Ribes L.	*Ribes glandulosum* Grauer	2	3	7		30	20

Ribes L.	*Ribes hirtellum* Michx.	2	1	2		18	4
Ribes L.	*Ribes hudsonianum* Richardson	2	1	9		23	60
Ribes L.	*Ribes hudsonianum* Richardson var. *petiolare* (Douglas) Jancz.	2	1	21		5	22
Ribes L.	*Ribes indecorum* Eastw.	2	2			12	2
Ribes L.	*Ribes inerme* Rydb.	2	2	18		10	27
Ribes L.	*Ribes inerme* Rydb. var. *klamathense* (Coville) Jeps.	2	2			1	
Ribes L.	*Ribes irriguum* Douglas (=*Ribes oxyacanthoides* subsp. *irriguum* (Douglas) Q. P. Sinnott)	2	2			3	
Ribes L.	*Ribes lacustre* (Pers.) Poir.	2	3	35		32	53
Ribes L.	*Ribes lasianthum* Greene	2	3			1	
Ribes L.	*Ribes laxiflorum* Pursh	2	2	8		16	11
Ribes L.	*Ribes leptanthum* A. Gray	2	2	3		11	6
Ribes L.	*Ribes lobbii* A. Gray	2	2	7		9	10
Ribes L.	*Ribes malvaceum* Sm.	2	2	5		23	8
Ribes L.	*Ribes menziesii* Pursh	2	2	3		15	3
Ribes L.	*Ribes mescalerium* Coville	2	2	3		1	3
Ribes L.	*Ribes missouriense* Nutt.	2	2	17		16	30
Ribes L.	*Ribes montigenum* McClatchie	2	2	8		10	17
Ribes L.	*Ribes nevadense* Kellogg	2	2	5		14	8
Ribes L.	*Ribes niveum* Lindl.	2	2	9		14	24
Ribes L.	*Ribes odoratum* H. L. Wendl. (=*Ribes aureum* var. *villosum* DC.)	2	1			74	2
Ribes L.	*Ribes oxyacanthoides* L.	2	1	3	1	14	5
Ribes L.	*Ribes oxyacanthoides* subsp. *irriguum* (Douglas) Q. P. Sinnott	2	1	5			5
Ribes L.	*Ribes oxyacanthoides* subsp. *setosum* (Lindl.) Q. P. Sinnott	2	1	1		4	1
Ribes L.	*Ribes pinetorum* Greene	2	2	2		5	2
Ribes L.	*Ribes quercetorum* Greene	2	2	6		6	9
Ribes L.	*Ribes roezlii* Regel	2	2	10		10	14

(continued)

Table 9.1 (continued)

Genus	Taxon	Ploidy	Gene pool	Number of accessions in NPGS[a]	Number of accessions in PGRC (Canada)[b]	Number of accessions in BGCI[c]	Number of accessions in GENESYS[d]
Ribes L.	*Ribes roezlii* var. *amictum* (Greene) Jeps.	2	2			2	1
Ribes L.	*Ribes roezlii* var. *cruentum* (Greene) Rehder	2	2	6		1	6
Ribes L.	*Ribes rotundifolium* Michx.	2	2	9		4	10
Ribes L.	*Ribes sanguineum* Pursh	2	1	29		85	38
Ribes L.	*Ribes sanguineum* Pursh var. *glutinosum* (Benth.) Loudon	2	1	2		18	4
Ribes L.	*Ribes sanguineum* Pursh var. *sanguineum*	2	1	2		5	4
Ribes L.	*Ribes speciosum* Pursh	2	2	2		47	5
Ribes L.	*Ribes thacherianum* (Jeps.) Munz	2	2	1		7	1
Ribes L.	*Ribes triste* Pall.	2	1	15		23	23
Ribes L.	*Ribes velutinum* Greene	2	2	4		4	8
Ribes L.	*Ribes viburnifolium* A. Gray	2	2	6		22	9
Ribes L.	*Ribes viscosissimum* Pursh	2	2	27		8	48
Ribes L.	*Ribes watsonianum* Koehne	2	2	1		6	3
Ribes L.	*Ribes wolfii* Rothr.	2	2	2		2	2
Rubus L.	*Rubus adenoleucus* Chaboiss.	2	3	2		1	3
Rubus L.	*Rubus allegheniensis* Porter	2, 3	1	39		29	47
Rubus L.	*Rubus alumnus* L. H. Bailey	3, 4	4	1		2	2
Rubus L.	*Rubus anglocandicans* A. Newton (introduced)	4	3	1		2	2
Rubus L.	*Rubus arcticus* L.	2, 3	1	4	1	33	8
Rubus L.	*Rubus arcticus* L. nothosubsp. *stellarcticus* G. Larss.	2	1	6			6
Rubus L.	*Rubus arcticus* L. subsp. *stellatus* (Sm.) B. Boivin	2	1			2	
Rubus L.	*Rubus arcticus* L. subsp. acaulis (Michx.) Focke	2	1			3	
Rubus L.	*Rubus arcticus* L. subsp. *arcticus*	2	1	7			7

Rubus L.	*Rubus arcticus* × *saxatilis*	2	1			1	
Rubus L.	*Rubus arcticus* × *stellatus*	2	1			1	
Rubus L.	*Rubus argutus* Link	2, 3, 4	1	7		3	9
Rubus L.	*Rubus arizonensis* (Greene.) Rydb.	0	1			1	
Rubus L.	*Rubus allegheniensis* Porter	2	2	39			
Rubus L.	*Rubus armeniacus* Focke (introduced)	4	1	25		3	26
Rubus L.	*Rubus baileyanus* Britton	?	2				1
Rubus L.	*Rubus bartonianus* M. Peck	4	3	3		2	2
Rubus L.	*Rubus canadensis* L.	2	1	17		4	17
Rubus L.	*Rubus chamaemorus* L.	8	1	29		23	48
Rubus L.	*Rubus cuneifolius* Pursh	2, 4	1	1		1	1
Rubus L.	*Rubus deliciosus* Torr.	2, 3	3	5		33	7
Rubus L.	*Rubus flagellaris* Willd.	4, 5, 7, 8, 9	2	12		19	14
Rubus L.	*Rubus frondosus* Bigelow	2, 3, 4	3			1	1
Rubus L.	*Rubus hawaiensis* A. Gray	2	3	14		4	15
Rubus L.	*Rubus hispidus* L.	2, 5, 8	2	11		12	15
Rubus L.	*Rubus idaeus* L. subsp. *strigosus* (Michx.) Focke	2	1	129			122
Rubus L.	*Rubus idaeus* L. var. *canadensis*	2	1			4	
Rubus L.	*Rubus idaeus* L. var. *strigosus* (Michx.) Focke	2	1		100	24	14
Rubus L.	*Rubus kennedyanus* Fernald	4	3	1		1	1
Rubus L.	*Rubus laciniatus* Willd. (introduced)	4	2	10		26	11
Rubus L.	*Rubus lasiococcus* A. Gray	2	3	10		1	14
Rubus L.	*Rubus leucodermis* Douglas ex Torr. & A. Gray	2	1	50		20	62
Rubus L.	*Rubus leucodermis* Douglas ex Torr. & A. Gray var. *bernardinus*	2	1			1	
Rubus L.	*Rubus leucodermis* Douglas ex Torr. & A. Gray var. *leucodermis*	2	1			1	
Rubus L.	*Rubus macraei* A. Gray	6	3			1	2

(continued)

Table 9.1 (continued)

Genus	Taxon	Ploidy	Gene pool	Number of accessions in NPGS[a]	Number of accessions in PGRC (Canada)[b]	Number of accessions in BGCI[c]	Number of accessions in GENESYS[d]
Rubus L.	*Rubus macvaughianus* Rzed. & Calderón	2	3	3		1	10
Rubus L.	*Rubus malifolius* (introduced)	?	3			3	
Rubus L.	*Rubus neglectus* Peck	2	1	15			15
Rubus L.	*Rubus neomexicanus* A. Gray	2	3	2		3	2
Rubus L.	*Rubus nivalis* Douglas	6	2	2		2	2
Rubus L.	*Rubus niveus* Thunb.	2, 4, 5	2	16		10	26
Rubus L.	*Rubus occidentalis* L.	2	2	227		30	260
Rubus L.	*Rubus odoratus* L.	2	3	11		125	18
Rubus L.	*Rubus parviflorus* Nutt.	2	3	32	1	69	42
Rubus L.	*Rubus parvifolius* L. (introduced)	2	1	37		27	50
Rubus L.	*Rubus pedatus* Sm.	2	3	14		9	20
Rubus L.	*Rubus pensilvanicus* Poir.	4	3	1		8	2
Rubus L.	*Rubus phoenicolasius* Maxim. (introduced)	2	1	4		56	12
Rubus L.	*Rubus praecox* Bertol. (introduced)	4	3	2		1	2
Rubus L.	*Rubus procerus* auct. (=*Rubus armeniacus* Focke) (introduced)	4	3			1	
Rubus L.	*Rubus pubescens* Raf.	2, 4	3	2		12	3
Rubus L.	*Rubus recurvans* Blanch.	3	3				1
Rubus L.	*Rubus repens* (=*Dalibarda repens* L.)	?	3			1	
Rubus L.	*Rubus riograndis* L. H. Bailey	4	2	1		1	1
Rubus L.	*Rubus semisetosus* Blanch.	?	3			1	1
Rubus L.	*Rubus spectabilis* Pursh	2	3	54	9	57	58
Rubus L.	*Rubus subtercanens* W.C.R. Watson (introduced)	2	3			1	1
Rubus L.	*Rubus trilobus* Ser.	2	2			5	

Rubus L.	*Rubus trivialis* Michx.	2, 3	1	25		7	29
Rubus L.	*Rubus ulmifolius* Schott (introduced)	4	2	25		34	64
Rubus L.	*Rubus ursinus* Cham. & Schltdl.	6, 8, 9, 10, 11, 12	1	84		17	79
Rubus L.	*Rubus urticifolius* Poir.	2	3	4		1	4
Rubus L.	*Rubus vermontanus* Blanch.	2	1	1		1	1
Vaccinium L.	*Vaccinium angustifolium* Aiton	4	1	61		75	66
Vaccinium L.	*Vaccinium arboreum* Marshall	2	1	30		32	42
Vaccinium L.	*Vaccinium boreale* I. V. Hall & Aalders	2	1	9		3	10
Vaccinium L.	*Vaccinium caesariense* Mack.	4	1	3		3	3
Vaccinium L.	*Vaccinium cespitosum* Michx.	4, 6	1	10		12	12
Vaccinium L.	*Vaccinium calycinum* Sm.	2	2	7		2	9
Vaccinium L.	*Vaccinium confertum* Kunth	2	3	1		3	
Vaccinium L.	*Vaccinium corymbosum* L.	2, 4, 6	1	290	18	133	494
Vaccinium L.	*Vaccinium crassifolium* Andrews	2	3	4		10	4
Vaccinium L.	*Vaccinium darrowii* Camp	2	1	44		9	83
Vaccinium L.	*Vaccinium deliciosum* Piper	4	2	11		8	12
Vaccinium L.	*Vaccinium elliottii* Chapm.	2	1	22		14	52
Vaccinium L.	*Vaccinium erythrocarpum* Michx.	2	3	7		6	6
Vaccinium L.	*Vaccinium formosum* Andrews	4	1	3		1	4
Vaccinium L.	*Vaccinium fuscatum* Aiton	2	1	22	1	17	26
Vaccinium L.	*Vaccinium hirtum* Thunb.	4	3	1		3	5
Vaccinium L.	*Vaccinium macrocarpon* Aiton	2	1	146	1	70	166
Vaccinium L.	*Vaccinium membranaceum* Douglas ex Torr.	2	1	71		20	81
Vaccinium L.	*Vaccinium myrsinites* Lam.	8	1	2		13	7
Vaccinium L.	*Vaccinium myrtilloides* Michx.	2	1	10		26	15

(continued)

Table 9.1 (continued)

Genus	Taxon	Ploidy	Gene pool	Number of accessions in NPGS[a]	Number of accessions in PGRC (Canada)[b]	Number of accessions in BGCI[c]	Number of accessions in GENESYS[d]
Vaccinium L.	*Vaccinium myrtillus* L.	2, 4, 6	1	43		98	332
Vaccinium L.	*Vaccinium ovalifolium* Sm.	4,6	1	93		36	117
Vaccinium L.	*Vaccinium ovatum* Pursh	2	3	35		48	41
Vaccinium L.	*Vaccinium oxycoccos* L.	2	3	77		66	203
Vaccinium L.	*Vaccinium pallidum* Aiton	2, 4	2	31		35	39
Vaccinium L.	*Vaccinium parvifolium* Sm.	2	3	38		29	49
Vaccinium L.	*Vaccinium reticulatum* Sm.	2	1	32		1	35
Vaccinium L.	*Vaccinium scoparium* Leiberg ex Coville	2	3	17		11	25
Vaccinium L.	*Vaccinium simulatum* Small	4	3	29		5	32
Vaccinium L.	*Vaccinium stamineum* L.	4	2	13		35	29
Vaccinium L.	*Vaccinium tenellum* Aiton	2	2	8		3	14
Vaccinium L.	*Vaccinium uliginosum* L.	2, (3), 4, 6	3	111	1	69	157
Vaccinium L.	*Vaccinium virgatum* Aiton	6	1	64	1	14	83
Vaccinium L.	*Vaccinium vitis-idaea* L.	2	1	108		116	184

[a] USDA, ARS (2017a)
[b] AAFC (2017)
[c] BGCI (2017)
[d] Global Crop Diversity Trust (2017)

9.2.3 Challenges in Cultivation: Pests, Diseases, and Edaphic and Climatic Limitations

Virus diseases are ubiquitous wherever strawberries are cultivated (Maas 1998). Extensive testing and certification programs have been developed for the strawberry nursery industry in many countries (Diekmann et al. 1994). The recommended procedures for detection of berry viruses include bioassays on indicator plants, sap and graft inoculation, enzyme-linked immunosorbent assay (ELISA), and double-stranded RNA detection with the polymerase chain reaction (PCR). Cultivated plantings should be started from certified pathogen-negative sources.

Common insects and diseases should be managed to maintain healthy and vigorous plants. Diekmann et al. (1994) and Maas (1998) describe symptoms, host range, geographical distribution, biology, and transmission of common strawberry diseases. Nearly 200 species of insects and mites have been reported to infect strawberry plants in North America (Maas 1998). Not only do arthropods cause direct plant damage, but they can also vector viruses and other diseases. Suggested control measures for arthropod pests combine cultural, biological, and chemical methods in an integrated plant production approach. These pests must be controlled in genebanks.

Abiotic stresses can be increased by factors as diverse as climate change and market dynamics. Changes in timing and duration of seasonal progressions can affect flowering time, movement of pollinators, and chilling hours.

9.2.4 Nutritional and Functional Use

Fresh strawberries are a low-calorie source of vitamin A, vitamin C, vitamin K, folate, potassium, dietary fiber, and polyphenols and other phytonutrients (USDA-NDL 2017). Most analytical biochemical studies of fruits have relied on specific extraction/separation methods to identify and quantify compounds of interest.

9.2.5 Crop Wild Relatives and Wild Utilized Species

9.2.5.1 Distribution, Habitat, and Abundance

Four strawberry species and two hybrid species are endemic to North America and Hawaii (Hummer et al. 2011; Lee 1964; Staudt 1999, 2009) (Table 9.1, Fig. 9.1). Strawberry species cover the North American landscape, ranging across Alaska and Canada in the north, along the western ocean beaches from Alaska through the fog zone of California, across the continent from West to East, and south through Mexico. *Fragaria chiloensis* (L.) Mill., the beach strawberry, is plentiful along sandy beaches of the Pacific Ocean from Alaska to California. *Fragaria chiloensis*

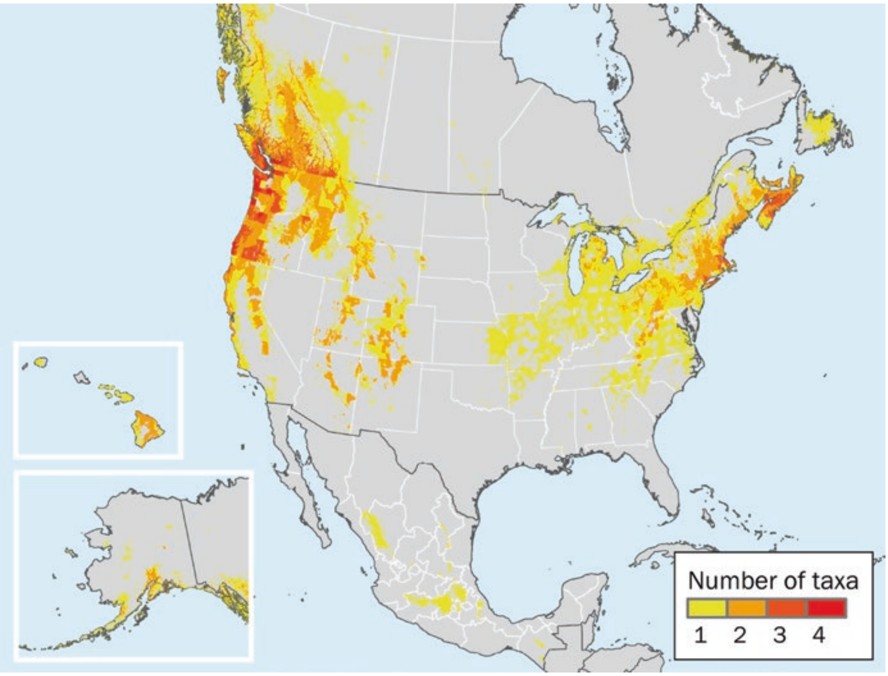

Fig. 9.1 Species richness map of modeled potential distribution of *Fragaria* taxa in North America, based on climatic and edaphic similarities with herbarium and genebank reference localities. Warmer colors indicate areas where greater numbers of taxa potentially occur in the same geographic localities. Full methods for generation of map and data providers are given in Appendix 1

(L.) Mill. subsp. *sandwicensis* (Decne.) Staudt is distributed in mountainous regions of the big island of Hawaii and on Maui (Staudt 1999). *Fragaria virginiana* Mill. is native throughout much of the USA and Canada.

Fragaria × *ananassa* Duchesne ex Rozier nothosubsp. *cuneifolia* (Nutt. ex Howell) Staudt is a natural hybrid of *F. chiloensis* (L.) Mill. subsp. *pacifica* Staudt or subsp. *lucida* (E. Vilm. ex Gay) Staudt and *F. virginiana* Mill. subsp. *platypetala* (Rydb.) Staudt (Staudt 1999) (Fig. 9.2). This hybrid has smaller leaves, flowers, and fruits than the cultivated strawberry. The distribution of *F.* × *ananassa* subsp. *cuneifolia* extends from the coastal regions of British Columbia (Vancouver Island), Canada, south to Fort Bragg and Point Arena lighthouse in California, USA. Hybrids of *F.* × *ananassa* subsp. *cuneifolia* and the two octoploids, *F. chiloensis* subsp. *pacifica* and *F. virginiana* subsp. *platypetala*, have been seen in Oregon, Washington, and California (Staudt 1999).

North American indigenous peoples used and consumed wild strawberries. Primarily, the whole plant of several species of strawberries, including the beach, the woodland (*F. vesca* L.), and the Virginia strawberries, were collected and used. Most of these plants were obtained for medicinal purposes. Moerman (2009) cites

Fig. 9.2 Flower and leaves of *Fragaria virginiana* Mill. subsp. *platypetala* (Rydb.) Staudt growing at the National Clonal Germplasm Repository, Corvallis, OR, USA. (Photo by K.E. Hummer, USDA ARS, 04/2011)

15 references for uses of strawberries by 11 tribes of indigenous peoples of North America. They were used as analgesic, antidiarrheal, dermatological, pediatric, gastrointestinal, kidney, liver, psychological, and sedative aids, as well as a remedy for toothache and a general disinfectant. Berries were also used as a deodorant. In some tribes the whole plant was kept in the home to ensure happiness. The plant was dried and used as a powder or poultice or prepared as a decoction of leaves or infusion of roots.

9.2.5.2 Utilization: North American Breeding Contributions

Research into trait discovery, including perpetual flowering and sex determination, in *Fragaria* species has been active since the eighteenth century (Richardson 1914). Many traits have been characterized, and genes associated with flowering (Gaston et al. 2013; Koskela et al. 2016), aroma, and flavor compounds (Chambers et al. 2014) have been cloned. Fruit firmness, a genetically complex trait, has been a focal point of many strawberry breeding programs during the past 50 years (Hancock et al. 2008b). As described by Salentijn et al. (2003), breeding to improve firmness and flavor simultaneously is a difficult task because of the inverse correlation between firmness and flavor volatiles. The increase in firmness developed through breeding has provided the industry with the capability to move fruit to the far reaches of the globe.

The flavor components of strawberries are complex. Schwab et al. (2009) summarize the genetic work concerning volatile and polyphenolic compounds, including metabolic routes and associated genetic mechanisms. The concentration of polyphenols varies among strawberry species and cultivars. Some breeding programs monitor the levels of these compounds to ensure maintenance of the already high levels. Other breeding programs favor development of cultivars that support year-round production and have fruit with good flavor to encourage increased consumption of an already nutritious fruit. Colquhoun et al. (2012) describe consumer preferences for sweetness and complex flavor in strawberry fruit.

Genetic linkage maps of diploid (Davis and Yu 1997; Sargent et al. 2006; Sargent et al. 2004) and octoploid (Bassil et al. 2015; Lerceteau-Köhler et al. 2012; van Dijk et al. 2014; Zorrilla-Fontanesi et al. 2011) populations have been developed using various marker types and platforms. Robust markers for molecular fingerprinting of species have been developed (Chambers et al. 2013), and the genome of the diploid woodland strawberry (*F. vesca*) has been sequenced (Shulaev et al. 2011). These advances provide tools for research and breeding of improved strawberry cultivars.

Since the mid-1800s, the efforts of over 35 breeding programs in Europe and the USA have resulted in thousands of cultivars (Faedi et al. 2000). In the late 1900s, strawberry breeding programs began in Asian countries and Oceania (Darrow 1966). During the past two decades, with the advent of improved genotypes and efficient knowledge-based cultivation techniques, private strawberry companies have globalized and now provide strawberries to markets in high population centers around the world, 365 days of the year. This multi-billion dollar success is predicated on the initial and continued improvement of cultivars resulting from the incorporation of wild germplasm into advanced cultivars through breeding.

Important historical breeders include the California breeders Albert Etter, Earl Goldsmith, Harold Thomas, and Harold Johnson (Sjulin 2006; Wilhelm and Sagen 1974). Their significant founding clones “Shasta,” “Sierra,” “Lassen,” “Tahoe,” “Donner,” and “Heidi” became the parental cultivars for subsequent public and private breeding programs in California. In the 1950s, Royce Bringhurst assumed management of the University of California strawberry breeding program, which had moved to the University of California, Davis (Hancock 2006a). He and his collaborator Victor Voth in southern California began breeding for large berries on plants adapted to California growing conditions. Bringhurst discovered a day-neutral *F. virginiana* Mill. subsp. *glauca* (S. Watson) Staudt (Fig. 9.3) growing in Hecker Pass, Utah. The day-neutral trait enabled production of strawberry fruit every day of the year somewhere in California. Strawberry breeders throughout the nation and throughout the world obtained this germplasm to breed cultivars with this valuable trait.

Additional traits have been transferred from wild North American genetic resources, including resistance to red stele (*Phytophthora fragariae* var. *fragariae* Hickman) and the strawberry aphid, drought and salinity tolerance, and winter hardiness. Other valuable traits that could be donated from wild American germplasm include higher photosynthetic rate, lower fertilizer requirement, heat tolerance, and resistance to soil pathogens and to powdery mildew. Hancock et al. (2010)

Fig. 9.3 Flower, flower buds, and leaves of *Fragaria virginiana* Mill. subsp. *glauca* (S. Watson) Staudt growing at the National Clonal Germplasm Repository, Corvallis, OR, USA. (Photo by K.E. Hummer, USDA ARS, 04/2011)

evaluated many American octoploids for their potential to expand the *F.* × *ananassa* gene pool. Stegmeir et al. (2010) identified hybrid genotypes from CWR that had high values for fruit color, firmness, and soluble solids, among other traits.

9.2.6 In Situ Conservation Status of CWR and WUS

NatureServe ranks the Hawaiian strawberry, *Fragaria chiloensis* subsp. *sandwicensis*, which is endemic on the islands of Maui and Hawaii, as globally imperiled (NatureServe 2017). The population sizes of *F. chiloensis* subsp. *lucida* (Fig. 9.4) and *F. vesca* L. subsp. *californica* (Cham. & Schltdl.) Staudt (Fig. 9.5), growing along the valuable California coast, are being reduced due to human encroachment and invasive species (Hancock, personal communication 2016).

9.3 Currants and Gooseberries (*Ribes* L.)

9.3.1 Origin and Brief History of Use

The genus *Ribes* is placed in the family Grossulariaceae (previously in Saxifragaceae) and includes about 150 species worldwide (Brennan 2008). Breeders have incorporated germplasm from about 18 species in the pedigrees of modern fruit cultivars of currants and gooseberries (Harmat et al. 1990). Additional species have commercial ornamental landscape application or potential.

Fig. 9.4 Flowers and leaves of *Fragaria chiloensis* (L.) Mill. subsp. *lucida* (E. Vilm. ex Gay) Staudt growing at the National Clonal Germplasm Repository, Corvallis, OR, USA. (Photo by K.E. Hummer, USDA ARS, 04/2011)

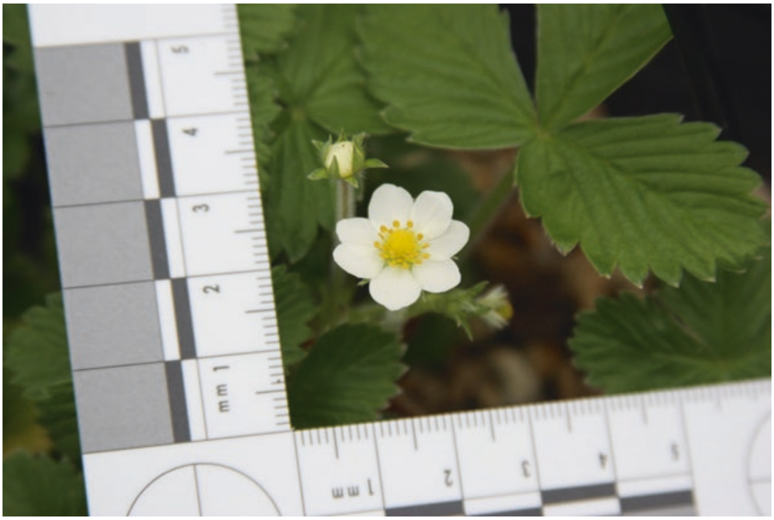

Fig. 9.5 Flower, flower buds, and leaves of *Fragaria vesca* L. subsp. *californica* (Cham & Schltdl.) Staudt growing at the National Clonal Germplasm Repository, Corvallis, OR, USA. (Photo by K.E. Hummer, USDA ARS, 04/2011)

Cultivated currants and gooseberries were initially derived from English and European species, although American species have been chosen as parents of the cultivated gooseberries to contribute disease resistance. For black currants, the primary species of commerce is *Ribes nigrum* L.; for red and white currants, *R. rubrum* L.; and for gooseberries, *R. uva-crispa* L.

The black currants were first selected for their fruits in the 1600s as recorded in early herbals (Brennan 1996). The first recorded cultivation of red and white currants for their fruit was in the 1400s and that of gooseberries in the 1200s. Recent improvements are the result of the crosses of black currant species with gooseberry species performed by Rudolf Bauer to produce the hybrid species *R.* × *nidigrolaria* Rud. Bauer & A. Bauer. "Josta," released in 1977, was the first of these types (Bauer 1986). Bauer released additional cultivars of this hybrid species so that cultivars of this group have become commonly known as jostaberries.

9.3.2 Modern-Day Use and Agricultural Importance

Globally, the most economically important *Ribes* crop is black currants. This crop is mechanically harvested for processing from intensive, large-scale farms, primarily in Russia, Ukraine, Poland, Austria, and France. World production varies from 500,000 to 600,000 MT annually with production in 2014 estimated at >659,000 MT (UNFAO 2017). The fruits are most often processed into juice, but other popular products include jams, jellies, liqueurs, and colorants used in yogurts and other dairy products. The main red currant producers are Poland and Germany. Germany, Russia, Poland, Ukraine, and the UK are the top producing countries for gooseberries with >170,000 MT produced in 2014. In North America, a small amount of acreage is used for growing black and red currants in Canada, the eastern USA, and Washington State, although not enough to be reported by the UNFAO (Hummer and Dale 2010).

9.3.3 Challenges in Cultivation: Pests, Diseases, and Edaphic and Climatic Limitations

While the major pest challenge for European black currant production is *Blackcurrant reversion virus*, this is not the case for North America. The European vector for this disease, the black currant gall mite [*Cecidophyopsis ribis* (Westw.)] (Adams and Thresh 1987), does not occur in North America (Brennan et al. 2009).

The key *Ribes* pest in North America is white pine blister rust (caused by *Cronartium ribicola* C J Fisher) (Barney and Hummer 2005). Originally from Asia, this rust was introduced into North America on infected white pine nursery stock in the late nineteenth and early twentieth centuries. It spread across North America during the early 1900s. This rust requires two co-hosts, a five-needle white pine and a currant or gooseberry, to complete its life cycle. To reduce infection of pines, *Ribes* production is prohibited or restricted by regulations in 12 states. Several black currant cultivars with resistance have been identified (Barney and Fallahi 2009; Barney and Hummer 2005).

Powdery mildew [*Podosphaera mors-uvae (Schwein.)*, formerly *Sphaerotheca mors-uvae*] is another primary problem in currant and gooseberry production plantations. Resistant cultivars are an effective control strategy. European gooseberries are most susceptible, followed by European black currants, American gooseberries, red and white currants, and jostaberries.

Common insect pests in North American *Ribes* and their origins include aphids [*Capitophorus ribis* L., North America and Europe; *Aphis grossulariae* Kalt., Europe; *Hyperomyzus pallidus* (H.R. L.) and *Nasonovia ribisnigri* (Mosley), Europe], currant borer (*Synanthedon tipuliformis*, North America), and gooseberry sawfly (*Nematus ribesii* Scop., North America).

9.3.4 Nutritional and Functional Use

Black currants are particularly rich in vitamin C, phenolics, anthocyanins, and other phytonutrients (Moyer et al. 2002). The primary anthocyanins present in black currants are 3-0-glucoside and 3-0-glutinoside. Black currant fruit extracts have been studied for use in cardiovascular health, as anticancer agents, to lower oxidative stress and postprandial glycemic responses (Mortaş and Şanlıer 2017).

9.3.5 Crop Wild Relatives and Wild Utilized Species

9.3.5.1 Distribution, Habitat, and Abundance

More than 50 *Ribes* species are native to North America (Table 9.1; Fig. 9.6). The Pacific Northwest in North America is a center of gooseberry species diversity.

Ribes species grow in a range of habitats in temperate woods and mountainous regions. They tend to be shade tolerant and can be found as elements of the understory in conifer forests and in disturbed sites along roadways and drainage ditches. Some species grow in moist areas or bogs.

Ribes species have been used medicinally for centuries. North American indigenous peoples used the fruits of wild currants and gooseberries as food, the inner bark as a poultice for sores and swelling, and the root for sore throats (Moerman 2009). *Gerard's Herbal*, an English herbal published in 1597, describes black and red currants and gooseberries and their medicinal uses (Woodward 1924).

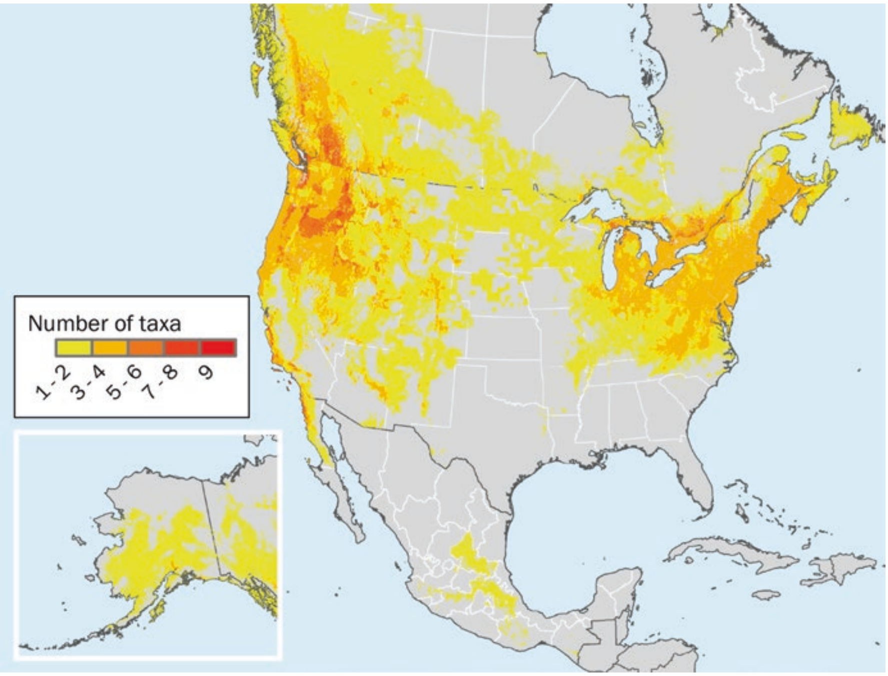

Fig. 9.6 Species richness map of modeled potential distribution of *Ribes* taxa in North America, based on climatic and edaphic similarities with herbarium and genebank reference localities. Warmer colors indicate areas where greater numbers of taxa potentially occur in the same geographic localities. Full methods for generation of map and data providers are given in Appendix 1

9.3.5.2 Utilization: North American Breeding Contributions

Active breeding programs are currently based in the UK, Russia, Poland, Estonia, Lithuania, and New Zealand (Brennan 2008). Early important cultivars include "Consort" from Canada that is resistant to white pine blister rust; "Laxton's No. 1," a red currant that is an important parent; and the "Ben" series of black currants from the UK breeding program in Scotland (Brennan 2008).

Genetic research into *Ribes* has revealed many species that have contributed key traits for improving cultivation (Barney and Hummer 2005; Brennan et al. 2009). The cluster length and yields of black currant cultivars have been improved by incorporating *Ribes bracteosum* Douglas ex Hook., the California black currant. *R. americanum* Mill. (Fig. 9.7), and the American black currant. These species also have the potential to provide powdery mildew resistance in interspecific hybrids (Brennan 2008). Other North American species that could broaden the gene pool are *R. hudsonianum* Richardson, the North American black currant, and *R. aureum* Pursh var. *villosum* DC. (Fig. 9.8), which has a large, sweet fruit that ripens much later than traditional black currant cultivars.

Fig. 9.7 Flowering branch of *Ribes americanum* Mill. growing at the National Clonal Germplasm Repository, Corvallis, OR, USA. (Photo by K.E. Hummer, USDA ARS, 04/2007)

Fig. 9.8 Flowering branch of *Ribes aureum* Pursh growing at the National Clonal Germplasm Repository, Corvallis, OR, USA. (Photo by K.E. Hummer, USDA ARS, 04/2007)

Fig. 9.9 (**a**) Flowering branch of *Ribes divaricatum* Douglas growing at the National Clonal Germplasm Repository, Corvallis, OR, USA. (**b**) Flower of *Ribes divaricatum* growing at the National Clonal Germplasm Repository, Corvallis, OR, USA. (Photos by K.E. Hummer, USDA ARS, 04/2007)

While the cultivated red currants have been derived from many European species (Barney and Hummer 2005), the North American red currant, *R. triste* Pall., has fruit quality similar to the European species but has not yet been utilized for breeding. The commercial gooseberry was primarily derived from the European gooseberry *R. uva-crispa* (synonym = *R. grossularia*) that is native to the UK. The North American gooseberry species *R. divaricatum* Douglas (Fig. 9.9), *R. hirtellum* Michx., and *R. oxyacanthoides* L. (Fig. 9.10) have contributed to improved disease resistance and decreased spines when bred with the larger fruited European species. Many North American gooseberry species have fuchsia-like flowers and are planted for their ornamental features (Brennan 1996).

Various methods have been used to develop molecular markers (Brennan et al. 2002; Cavanna et al. 2009; de Mattia et al. 2008; Russell et al. 2011, 2014) and to create linkage maps (Brennan et al. 2008; Russell et al. 2014) for *Ribes*.

Fig. 9.10 Flowering branch of *Ribes oxyacanthoides* L. growing at the National Clonal Germplasm Repository, Corvallis, OR, USA. (Photo by K.E. Hummer, USDA ARS, 04/2007)

9.3.6 In Situ Conservation Status of CWR and WUS

Ribes echinellum (Coville) Rehder, the Miccosukee gooseberry (Fig. 9.11), is listed as threatened by the US Fish and Wildlife Service (2015) and critically imperiled by NatureServe (2017). It is known only from the two localities of Jefferson County, Florida (USA), near Lake Miccosukee, and McCormick County, South Carolina (US); thus it is vulnerable to human encroachment and regional development in the areas. The PLANTS Database (USDA-NRCS 2017) lists 12 additional *Ribes* taxa of concern under state laws in a total of 13 states.

9.4 Raspberries and Blackberries (*Rubus* L.)

9.4.1 Origin and Brief History of Use

The genus *Rubus*, a member of the rose family (Rosaceae), is one of the most diverse in the plant kingdom. More than 740 named species have been divided into 15 subgenera, including artificial hybrid groups (USDA, ARS 2017a). Raspberries

Fig. 9.11 Flowering branch of *Ribes echinellum* (Coville) Rehder growing at the National Clonal Germplasm Repository, Corvallis, OR, USA. (Photo by K.E. Hummer, USDA ARS)

and blackberries are the economically important cultivated crops in the genus. Red raspberry cultivation for fruit became widespread in European countries by the sixteenth century (Jennings 1988). Red raspberries have been selected mostly from European species, but the American red raspberry subspecies, *R. idaeus* L. subsp. *strigosus* (Michx.) Focke (synonym = *R. strigosus* Michx.), has significantly contributed to the cultivated red raspberry gene pool. Black raspberry cultivars were developed from the eastern North American black raspberry, *R. occidentalis* L. Purple raspberries (hybrids of black raspberry with red raspberry) were also developed from American germplasm.

Blackberry species, while distributed in Europe and America, were most intensely selected and bred from the widely diverse forms of American species. Cultivars developed in the USA were derived from different multi-species, germplasm pools centered in either the Pacific coastal regions or east of the Rocky Mountains. Innovative breeding has produced hybrid berries, combining blackberry and raspberry species, despite great ploidy incongruities.

9.4.2 Modern-Day Use and Agricultural Importance

Russia, Poland, the USA, Serbia, and Mexico are the top producing countries for red raspberries, with >612,570 MT produced in 2014. Black raspberry production is much less, ~900 MT, and production is centered in Oregon (USDA-ERS 2018), although a great deal of fruit is grown or imported for production of liqueurs in Korea.

Blackberry production is not large enough to be recorded through the UNFAO statistical database. Strik et al. (2007) surveyed world production of blackberries and reported 140,292 MT in 2005, with production increasing. The central highlands of Mexico have seen a dramatic increase in production for export of off-season fresh fruit into the USA, and they are now the world's leading blackberry producer.

9.4.3 Challenges in Cultivation: Pests, Diseases, and Edaphic and Climatic Limitations

Spotted wing drosophila (*Drosophila suzukii* Matsumura), a recent introduction to berry production areas outside of eastern Asia, has become a devastating problem for many berry growers, especially those growing raspberries and blackberries (Bolda et al. 2010). At this time, there are no known sources of resistance in wild germplasm.

Virus diseases are found throughout *Rubus*-growing regions and can be transmitted via insects, nematodes, or pollen (*Compendium of Raspberry and Blackberry Diseases and Pests* 2017). In red raspberry, *Raspberry bushy dwarf virus*, verticillium wilt, phytophthora root rot, and powdery mildew are among the biggest disease concerns. Black raspberry growers face similar disease problems, and *Black raspberry necrosis virus* is a serious problem for growers.

Generally, blackberries have fewer devastating diseases than raspberries; however, in newer, generally warmer production areas, new-to-blackberry diseases such as *Fusarium oxysporum* Schltdl. 1824 (Gordon et al. 2015) have become a problem. Efforts are being made by the breeding community to identify and incorporate genetic sources of resistance to virus vectors, especially aphids (Bushakra et al. 2015; Dossett and Finn 2010; Dossett and Kempler 2012) and diseases.

High temperatures and/or intense ultraviolet light can injure ripening raspberry and blackberry fruit, and there is a genetic variability for tolerance to these stresses (Finn and Clark 2012). Breeding efforts are going into improving plant tolerances to heat, cold, and drought to expand and extend the growing range.

9.4.4 Nutritional and Functional Use

Raspberries and blackberries are low-calorie sources of dietary fiber, calcium, potassium, vitamin A, vitamin C, vitamin K, and folate (USDA-NDL 2017). Whole fruits and fruit extracts of the cultivated *Rubus* species have been shown to decrease cancer cell proliferation in animal models (Ash et al. 2011; Mace et al. 2014; Montrose et al. 2011; Rodrigo et al. 2006; Stoner et al. 2005, 2007; Zhang et al. 2011; Zikri et al. 2009).

9.4.5 Crop Wild Relatives and Wild Utilized Species

9.4.5.1 Distribution, Habitat, and Abundance

Rubus species are diverse in morphology, cytology, and genetics. The GRIN database lists 34 species native to North America. The *Rubus* treatment in the Flora of North America (Alice et al. 2015) reports 27 *Rubus* species native to North America, with eight species introduced from Europe or Asia (Table 9.1, Fig. 9.12). Because *Rubus* is one of the most taxonomically challenging of plant genera (Aalders and Hall 1966; Alice and Campbell 1999), many names of species have been published and submerged as synonyms. Species definition is complicated by hybridization, polyploidy, agamospermy, and lack of a universal species concept (Alice and Campbell 1999).

Indigenous peoples of North America have used *Rubus* species for a range of edible and medicinal purposes (Moerman 1996; USDA-NRCS 2017). For example, the bark and leaves of salmonberry (*R. spectabilis* Pursh) (Fig. 9.13) were used in various ways to relieve general pain and relieve labor pains and as an antiseptic (Stevens and Darris 2003).

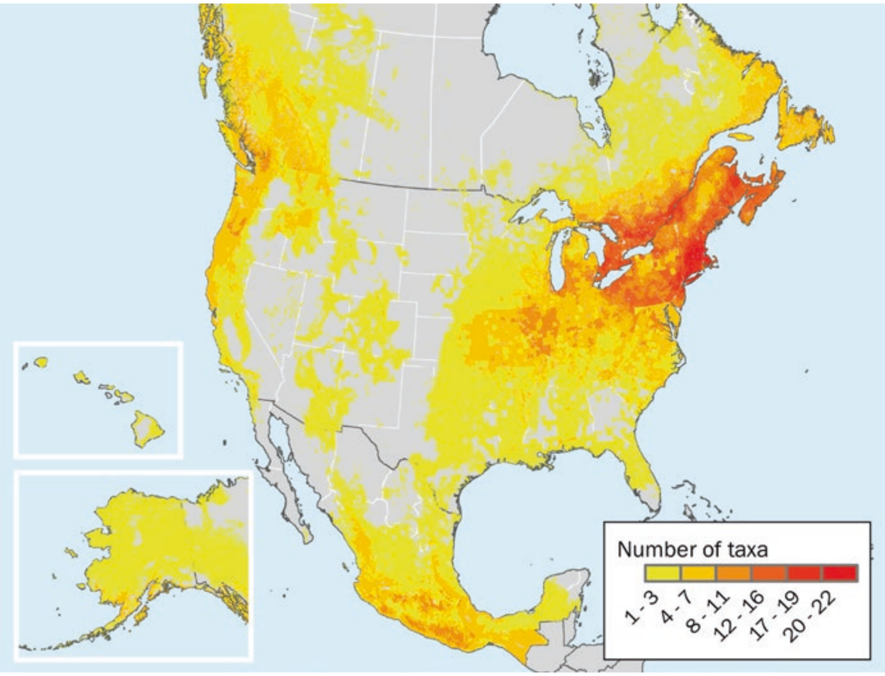

Fig. 9.12 Species richness map of modeled potential distribution of *Rubus* taxa in North America, based on climatic and edaphic similarities with herbarium and genebank reference localities. Warmer colors indicate areas where greater numbers of taxa potentially occur in the same geographic localities. Full methods for generation of map and data providers are given in Appendix 1

Fig. 9.13 Ripening fruit and leaves of *Rubus spectabilis* Pursh growing in the wild in Oregon. (Photo by K.E. Hummer, USDA ARS)

The many species of *Rubus* are adapted to different climates and growing conditions (Daubeny 1996; Thompson 1995). They can be found in the forest understories, disturbed habitats, and wetlands and are often pioneer species that can become weedy and invasive (Amsellem et al. 2001; Caplan and Yeakley 2013). At least eight European and Asian species have been introduced into North America and are now naturalized in the USA.

9.4.5.2 Utilization: North American Breeding Contributions

Public North American breeding programs for *Rubus* are based primarily at the University of Arkansas and the USDA-ARS in Corvallis, Oregon. Newer public breeding programs are housed at the University of North Carolina; the USDA-ARS in Poplarville, Mississippi; and Agriculture and Agri-Foods Canada in Agassiz, British Columbia. Important early North American cultivars include red raspberry “Lloyd George,” “Early Red,” “Meeker,” “Washington,” and “September”; black raspberry “Munger” (Fig. 9.14), “Jewel,” and “Bristol”; and blackberry “Brazos,” “Darrow,” “Thornfree,” and “Eldorado” (Jennings 1988).

Of the 34 species listed in GRIN-Global as native to North America, 15 have been used in breeding (USDA, ARS 2017b). While the predominant germplasm resource for the development of the cultivated red raspberry has been the European *R. idaeus*, North American *R. idaeus* subsp. *strigosus* crosses freely with this material and has been a source of disease resistance and adaptive traits

Fig. 9.14 Fruit of black raspberry cultivar Munger. (Photo from USDA NCGR)

(Daubeny 1996; Jennings et al. 1991; Weber 2013). The germplasm pool used in black raspberry breeding has been all North American in origin and was extremely narrow until recently (Dossett 2011; Dossett et al. 2012a, b; Weber 2003). Recent *R. occidentalis* collections and evaluations have brought a wealth of diversity for vegetative and reproductive traits as well as aphid resistance, which can convey virus resistance, into breeding programs (Bushakra et al. 2015; Dossett 2011; Dossett and Finn 2010).

In the eastern USA, *R. allegheniensis* and *R. argutus* have been the primary species used to develop the erect and semi-erect-type blackberries, while in the west, *R. ursinus* has been the most important species contributing to the development of the trailing-type blackberries (Clark and Finn 2011; Clark et al. 2007; Finn 2001; Finn and Clark 2012). These North American raspberry and blackberry species have been collected and evaluated with varying degrees of rigor but provide a diverse and valuable source of germplasm that can readily be incorporated into advanced breeding material.

Breeding with these species has resulted in cultivars with introgressed traits from wild relatives. Current breeding programs are interested in improving fruit quality (flavor, skin firmness, color, color retention), postharvest characteristics (reduced fruit color reversion in blackberry, shelf life), yield, machine-harvest ability, and tolerance to biotic and abiotic stresses.

Research into trait discovery in *Rubus* species has been active since 1931. Studies were conducted on many species to identify if traits were controlled by single loci or controlled quantitatively (reviewed by Daubeny (1996)). Many traits have been characterized, although no genes have been identified. Recent advances in genome sequencing technologies are bringing us closer to gene discovery. The black raspberry genome sequence (VanBuren et al. 2016) and genetic linkage maps (Bushakra et al. 2015; Bushakra et al. 2012), red raspberry genetic linkage maps

(Graham et al. 2004; Sargent et al. 2007; Ward et al. 2013; Woodhead et al. 2010), and blackberry genetic linkage maps (Castro-Lopez et al. 2013) and expressed sequence tag libraries of *Rubus* sp. (Garcia-Seco et al. 2015; Lewers et al. 2008) are narrowing the focus for gene identification. Researchers now have a large molecular toolbox with which to address questions on genetics, genomics, and breeding of these important berry crops.

9.4.6 In Situ Conservation Status of CWR and WUS

The PLANTS Database (USDA-NRCS 2017) lists 17 *Rubus* species as having protected status in a total of 14 US states and Canadian provinces. *Rubus aliceae* L. H. Bailey is presumed to be globally extinct (NatureServe 2017). *Rubus bartonianus* M. Peck (Fig. 9.15), endemic to western Idaho and eastern Oregon, is ranked by NatureServe (2017) as globally imperiled. The two Hawaiian species, *Rubus hawaiensis* A. Gray (Fig. 9.16) and *R. macraei* A. Gray, are also ranked as globally imperiled. These two species are the only *Rubus* species endemic to the Hawaiian Archipelago, although five introduced species encroach upon their niche (Howarth et al. 1997; Morden et al. 2003).

Fig. 9.15 Flowering branch of *Rubus bartonianus* M. Peck collected from the Snake River Canyon, ID. (Photo by K.E. Hummer, USDA ARS)

Fig. 9.16 Flowers and ripening fruit of *Rubus hawaiensis* A. Gray growing in the wild. (Photo by J.D. Postman, USDA ARS)

9.5 Blueberries, Cranberries and Lingonberries (*Vaccinium* L.)

9.5.1 Origin and Brief History of Use

Vaccinium is a member of the heath family (Ericaceae). More than 450 *Vaccinium* species have been described in more than 31 subgenera (Song and Hancock 2011), although the taxonomy of the genus is controversial (Vander Kloet 2004). North American *Vaccinium* species have been improved through selection and breeding to become economically important cultivated crops (Brazelton and Young 2017).

The three main crops of commerce are blueberries (*V. corymbosum* L. and hybrids, *V. angustifolium* Aiton, and *V. virgatum* Aiton [synonym = *V. ashei* J.M. Reade]), cranberries (*V. macrocarpon* Aiton), and lingonberries (*V. vitis-idaea* L.); most of the *V. angustifolium* and *V. vitis-idaea* are harvested from managed wild stands. Blueberries were derived initially from section *Cyanococcus*, predominantly from selections and hybrids of *V. corymbosum*, the highbush blueberry); these North American-derived blueberries have been selected for many climatic regions and are now globally produced and grown. Selections of elite wild northern highbush blueberry (Coville 1921) led to the establishment of field plantations, and breeding to improve fruit production has been underway for the past 100 years. In the latter half of the twentieth century, breeders began to incorporate the southern US species *V. darrowii* Camp into breeding material to develop blueberries with a low chilling requirement (Hancock et al. 2008a). The development of blueberries that could be grown in no-chill or low-chill environments has been the most important development in blueberry since the release of the first cultivars 100 years ago as it has allowed the rapid expansion of the crop into new regions.

The American cranberry (*V. macrocarpon*), a diploid, is native to eastern North America. When colonists arrived in Massachusetts in 1614, they found and described these large-fruited cranberries growing on the peat bogs of Cape Cod (Eck 1990) and were taught by the indigenous peoples of the area to prepare food from them. The American cranberry was first domesticated and cultivated in Cape Cod in 1810. Breeding and research efforts have been conducted over the past 100 years for improvement of cranberry cultivation (Hancock et al. 2008a). Modern cultivated cranberries are wild selections of *V. macrocarpon* or cultivars specifically bred to be grown in managed bogs. Some efforts at field cultivation have been made but have not been successful on an ongoing large scale.

Most lingonberries (*V. vitis-idaea*) are harvested from the wild. While most cultivars are superior selections from the wild, cultivars have also been developed by breeding programs. This species is native in northern Canada and the USA. Cultivated production of lingonberries is under trial in the USA but has not been very successful.

Efforts to cultivate other native *Vaccinium* species, such as the oheloberry (*V. reticulatum* Sm.) (Figs. 9.17 and 9.18) and its wild relatives endemic to Hawaii, are in the early stages (Hummer et al. 2012).

9.5.2 Modern-Day Use and Agricultural Importance

In 2014, the USA, Canada, Mexico, Poland, and Germany were the top producing countries for blueberries, with a total of 525,621 MT. In 2014, a global total of 303 MT of cultivated and wild blueberries, valued at $824.9 million, were produced and utilized (USDA-NASS 2015). In 2015, the leading US state for production was Washington, followed by Oregon, Georgia, and Michigan (USDA-ERS 2018). Maine is the leading producer of lowbush "wild" blueberries that are gathered from managed native stands rather than cultivated fields. Fresh and processed wild blueberries were valued at $47.2 million in the USA in 2015.

In 2015, the value of the American cranberry crop was about $267 million (USDA-ERS 2018) for about 8.6 million barrels of fruit. Production was slightly higher in 2015 than in the previous year. Massachusetts, New Jersey, Oregon, Washington, and Wisconsin have the greatest production in the USA. This crop is now grown on approximately 40,000 acres (> 16,000 ha) across Canada and the northern USA (Song and Hancock 2011). Plantings are expanding in British Columbia, Michigan, Nova Scotia, Quebec, Chile, and Germany.

Fig. 9.17 Plant of *Vaccinium reticulatum* Sm. growing on lava in Hawaii, USA. (Photo by K.E. Hummer, USDA ARS)

9.5.3 Challenges in Cultivation: Pests, Diseases, and Edaphic and Climatic Limitations

Spotted wing drosophila (SWD) is the greatest threat to blueberry and other soft fruit production in the USA. There is a zero tolerance threshold for SWD larvae in fresh market fruit, and potential berry crop losses can be as high as $511 million annually in western states (Bolda et al. 2010). No one has yet found sources of resistance to this pest.

Throughout North America, blueberry production is threatened by many viruses that are regionally located. Some of the most important viruses include *Blueberry shoestring virus*, *Tomato ringspot virus*, *Tobacco ringspot virus*, *Blueberry leaf mottle virus*, *Blueberry red ringspot virus*, blueberry stunt phytoplasma, *Blueberry scorch virus*, and *Blueberry shock virus* (Martin et al. 2012).

Fig. 9.18 Branch with fruits and flowers of *Vaccinium reticulatum* Sm. growing at the National Clonal Germplasm Repository, Corvallis, OR, USA. (Photo by K.E. Hummer, USDA ARS)

In terms of climatic limitations in North America, blueberry germplasm has a range of environmental adaptations, with the exceptions of tolerance to the coldest regions of the north and to hot dry conditions. During the past 100 years, innovative breeders have combined North American CWR with the highbush blueberry to produce named cultivars for a range of environments. Blueberries were first selected from cold-hardy, northeastern-adapted elite clones from New Hampshire and New Jersey (Coville 1937). Now growers can plant blueberries throughout many climatic zones of North America, ranging from areas with minimum temperatures of about −40 °C to freeze-free locations when sufficient moisture is present. Breeders have been collaborating to evaluate mineral soil adaptation in blueberry cultivars (Scheerens et al. 1999a, b). Grafting cultivars onto mineral-adapted rootstock is another approach (Basey 2017).

Cranberry plants and fruit are affected by several major fungal diseases including root rots caused by *Phytophthora cinnamomi*; diebacks caused by *Phomopsis vaccinia*, *Fusicoccum putrefaciens*, and *Synchronoblastia crypta*; and leaf spots caused by *Pyrenobotrys compacta* and *Protoventuria myrtilli*. In addition, ringspot virus and false blossom phytoplasma reduce plant growth and yield. Insect pests include the black-headed fireworm *Rhopobota naevana* (Hübner), cranberry fruitworm

(*Acrobasis vaccinii* Riley), Sparganothis fruitworm (*Sparganothis sulfureana* Clemens), cranberry weevils (*Anthonomus musculus* Say), cutworms, and green and brown span worm.

9.5.4 Nutritional and Functional Use

Vaccinium fruits are a healthful and nutritious food for humans. The fruits are low in fat and salt content and contain only about 80 calories per cup. The berries contain phytonutrients called polyphenols including the pigments called anthocyanins. Blueberries have high contents of vitamin C, manganese, and dietary fiber and are preserved as jams, jellies, and syrups. The North American cranberry also has multiple health benefits linked to phytochemicals in the fruit (Neto et al. 2008).

9.5.5 Crop Wild Relatives and Wild Utilized Species

9.5.5.1 Distribution, Habitat, and Abundance

Crop wild relatives of blueberries are a diverse taxonomic group. The genus is polyphyletic (Kron et al. 2002), and species delineation is taxonomically complex (Song and Hancock 2011). A global taxonomic reassessment of the definition of the genus is needed. About 34 species of *Vaccinium* are indigenous to North America (Table 9.1, Fig. 9.19), many of which have been gathered from the wild for centuries by Native Americans.

Lowbush blueberry, sometimes called “wild” or “Maine” blueberry, is harvested from managed wild mixed stands of unselected *V. angustifolium* and *V. myrtilloides* Michx. genotypes throughout northeastern North America. While mostly grown in commercial fields today, *V. corymbosum* and *V. virgatum* were historically harvested by indigenous people, and pickers still harvest from the wild.

The little leaf cranberry, *V. oxycoccos* L., with a polyploid series from diploid to hexaploid, has a broad, circumboreal distribution. It is gathered from wild stands in Russia and Eastern Europe and across North America and, as in the cases of lingonberry and lowbush blueberry, has not undergone breeding for domestication.

Blueberry plants are shrubs, small trees, or vines that grow on acidic, sandy, peaty, or organic soils. They are pioneer plants, expanding in disturbed regions, on the edges of forests, where burning has occurred or where the upper tree story has been cut. Some temperate species, but not the highbush blueberry species, tend to grow in large clonal colonies with intricate, fibrous, and shallow rhizomes that can spread over large areas under forest or in open fields.

The American cranberry is a woody perennial vine that is found in sphagnum bogs, swamps, mires, wet shores, headlands, and upland meadows. It has a

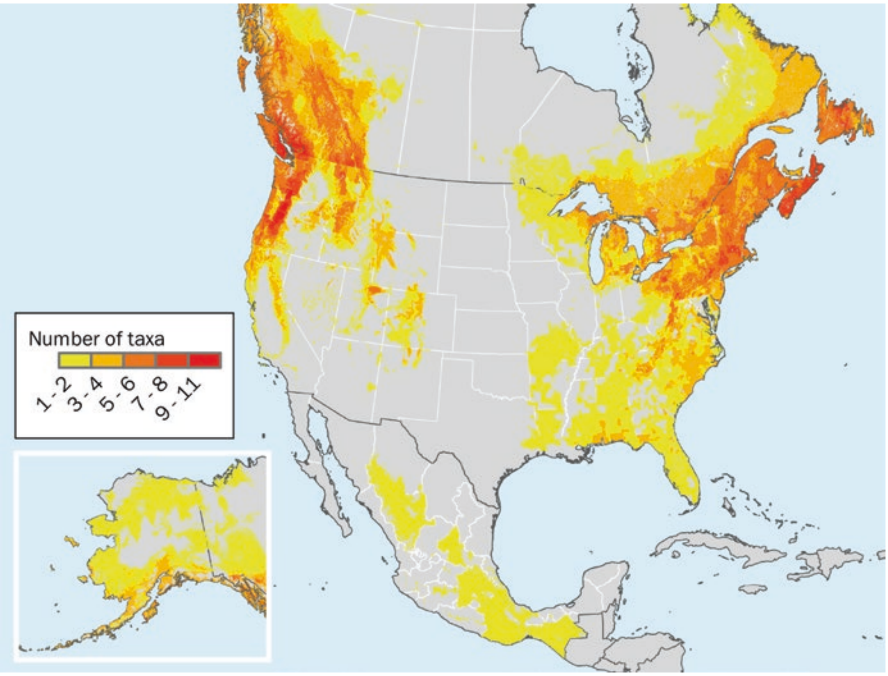

Fig. 9.19 Species richness map of modeled potential distribution of *Vaccinium* taxa in North America, based on climatic and edaphic similarities with herbarium and genebank reference localities. Warmer colors indicate areas where greater numbers of taxa potentially occur in the same geographic localities. Full methods for generation of map and data providers are given in Appendix 1

widespread distribution in eastern Canada and the northeastern and north-central USA, and south to the Appalachian Mountains of eastern Tennessee and North Carolina.

9.5.5.2 Utilization: North American Breeding Contributions

In North America, the highbush blueberry, *V. corymbosum* (Fig. 9.20), has been bred for 107 years, with significant historical contributions from Frederick Coville, George Darrow, and Arlen Draper (Hancock 2006b). Coville initiated highbush blueberry breeding in 1909 and produced “Bluecrop,” “Jersey,” and “Rubel” and many others. Darrow worked to understand the interspecific crosses and taxonomy. Arlen Draper extensively used native material in his crosses and was able to make crosses between individuals of different ploidy to produce, among others, the very important US 75 and “O’Neal.” Breeders have chosen a wide range of species within section *Cyanococcus* to develop hybrids with the highbush blueberry that are adapted to a broad range of environments: from the cold north to hot climates without winter. The tetraploid lowbush blueberry, *V. angustifolium*, was crossed with the

Fig. 9.20 Fruiting shrub of *Vaccinium corymbosum* L. growing at the National Clonal Germplasm Repository, Corvallis, OR, USA. (Photo by K.E. Hummer, USDA ARS)

highbush to create half-high blueberries that survive winter by growing beneath the snow line. In contrast, southern-adapted species, such as *V. darrowii*, were incorporated to produce plants whose buds require much fewer dormant chilling hours to successfully break and develop. New "evergreen" production systems allow fruit development at any time throughout the year in subtropical-tropical locations. These interspecific crosses created cultivars that facilitated robust production from Canada to Mexico thanks to genes contributed from North American germplasm.

Northern highbush blueberries are primarily selected from elite plants of tetraploid *V. corymbosum* or crosses between them. Southern highbush blueberries are hybrids of the northern *V. corymbosum* crossed with a combination of southern species such as *V. darrowii* (Fig. 9.21), so that they are adapted to conditions with fewer winter chilling hours. Rabbiteye blueberries are selections of *V. virgatum* that originally were bred and cultivated in southern North America but now are bred by a number of breeding programs and grown in other areas like the Pacific Northwest that are mild wintered, where they ripen extremely late.

Genetic research into *Vaccinium* species has led to the development of linkage maps for diploid (Rowland et al. 2014) and tetraploid (McCallum et al. 2016) blueberry populations based on various marker types (Bian et al. 2014; McCallum et al. 2016). The tetraploid blueberry genome has been sequenced and annotated (Gupta et al. 2015). The genome of cranberry has been sequenced (Polashock et al. 2014). Genetic linkage maps have been constructed for cranberry (Georgi et al. 2013) based on various marker types (Covarrubias-Pazaran et al. 2016; Fajardo et al. 2013; Schlautman et al. 2015).

Fig. 9.21 *Vaccinium darrowii* Camp growing in the wild in Florida. (Photo by Paul Lyrene, 05/2007)

Beginning in 1929, cultivars of the American cranberry were first bred by the United States Department of Agriculture-Agricultural Research Service (USDA-ARS) working with the New Jersey and Massachusetts Agricultural Experiment Stations. They began their breeding programs with selections from wild stands in Massachusetts, New Jersey, and Wisconsin. Today cranberry breeding efforts are focused on early fruit with a uniformly large size. Major cranberry breeding efforts continue in New Jersey, Wisconsin, and Massachusetts.

9.5.6 In Situ Conservation Status of CWR and WUS

The USDA Plants Database (USDA-NRCS 2017) lists 11 *Vaccinium* species, including *V. boreale* I.V. Hall & Aalders, northern blueberry, with some type of protected status in a total of 15 states. The limited distribution of *V. boreale* is protected in Maine and New York. Populations of *V. boreale* are not threatened in Canada (NatureServe 2017). *Vaccinium crassifolium* Andrews subsp. *sempervirens* (D. A. Rayner & J. Hend.) W. B. Kirkman & Ballington is listed as endangered in

Fig. 9.22 Bog of *Vaccinium macrocarpon* Aiton at Green Pond, George Washington National Forest, VA, USA. (Photo by K.A. Williams, USDA ARS)

South Carolina, where it is endemic, and ranked as critically imperiled by NatureServe (2017). *Vaccinium macrocarpon*, the American cranberry, is endangered in Illinois and threatened in Tennessee. The limited populations in these states warrant protection.

Vaccinium macrocarpon (Fig. 9.22) and *V. oxycoccos* (Fig. 9.23), the two native species of cranberry, are the focus of a project to identify sites for in situ conservation under the *US Forest Service(USFS)/Agricultural Research Service (ARS) Joint Strategic Framework on the Conservation and Use of Crop Wild Relatives in the United States*. Collaborators from the USFS, the USDA-ARS, and the University of Wisconsin have identified and documented populations of these species on National Forests and conducted population genetic analyses using molecular markers.

9.6 Ex Situ Conservation Status of CWR and WUS of Berry Species

The Multilateral System (MLS) of access and benefit sharing established by the International Treaty on Plant Genetic Resources for Food and Agriculture (ITPGRFA 2017) covers genetic resources of the crops listed in its Annex 1. Strawberry, which was recognized as a crop of global horticultural significance, is

Fig. 9.23 Fruiting branch of *Vaccinium oxycoccos* L. from the Olympic Peninsula, WA, USA. (Photo by K.A. Williams, USDA ARS)

included, but the other berry crops are not because they were not recognized as globally significant in 2004 when the ITPGRFA was established. A global conservation strategy for strawberry genetic resources was developed through the cooperation of the Global Crop Diversity Trust, the Bioversity International, the International Society for Horticultural Science, and international scientists (Hummer 2008).

The largest ex situ collection of North American berry genetic resources is held at the US national berry genebank located at the USDA-ARS National Clonal Germplasm Repository (NCGR) in Corvallis, Oregon. Their collection includes a broad diversity of *Fragaria*, *Ribes*, *Rubus*, and *Vaccinium* of not only North American taxa (Table 9.1) but also representatives of global species and cultivars (Postman et al. 2006; USDA, ARS 2017a). Primary collections are maintained on-site as living plants. Backup secondary collections of subgroups are maintained in different forms. Medium-term tissue cultures are maintained on-site and remotely; meristems have been placed in cryogenic storage at the base location, USDA-ARS National Laboratory for Genetic Resource Preservation, Ft. Collins, CO, USA. Protocols for dormant bud preservation in cryopreservation are under research (Jenderek et al. 2011).

At the NCGR, primary collections of major taxa are maintained in containers in screenhouses or planted in the field. Seed lots are stored in −18 °C. Plants are tested for common viruses, viroids, and phytoplasmas as funding allows. Plant identity is checked by comparison with written description, review by botanical and horticultural taxonomic experts, and evaluation by molecular markers, such as simple sequence repeat markers. Single nucleotide polymorphism (SNP) markers and genotyping by sequencing (GBS) approaches are being tested.

The collections have been documented for accession, inventory, voucher images, and morphological and genetic observations on the Germplasm Resources Information Network (USDA, ARS 2017a). Accessions of more than 22,770 strawberry, 9,900 currant and gooseberry, 14,800 blackberry and raspberry, and 12,700 blueberry, cranberry, and lingonberry CWR have been distributed to international and domestic requestors from NCGR-Corvallis during the past four decades.

Other collections of berry genetic resources are conserved by the Canadian Clonal Genebank, botanic gardens in the Botanical Gardens Conservation International (BGCI) network, and genebanks whose holdings are listed in GENESYS (GCDT 2017) (Table 9.1). Other international genebanks have invested only limited conservation efforts for small fruit and temperate berry CWR.

References

Aalders LE, Hall IV (1966) A cytotaxonomic survey of the native blackberries of Nova Scotia. Can J Genet Cytol 8(3):528–532

Adams AN, Thresh JM (1987) Reversion of black currant. In: Converse RH (ed) Virus diseases of small fruits, vol 631. United States Department of Agriculture, Washington, DC, pp 133–136

AAFC Plant Gene Resources of Canada (2017) Germplasm Resources Information Network-Canadian Version (GRIN-CA) database. Plant Gene Resources of Canada, Saskatoon, SK. http://pgrc3.agr.gc.ca/search_grinca-recherche_rirgc_e.html. Accessed 18 Jan 2017

Alice LA, Campbell CS (1999) Phylogeny of *Rubus* (Rosaceae) based on nuclear ribosomal DNA internal transcribed spacer region sequences. Am J Bot 86(1):81–97

Alice LA, Goldman DH, Macklin JA, Moore G (2015) *Rubus*. In: F. o. N. A. E. Committee (ed) Flora of North America, vol 9. New York and Oxford. Retrieved from http://www.efloras.org/florataxon.aspx?flora_id=1&taxon_id=128837

Amsellem L, Dutech C, Billotte N (2001) Isolation and characterization of polymorphic microsatellite loci in *Rubus alceifolius* Poir. (Rosaceae), an invasive weed in La Réunion island. Mol Ecol Notes 1(1–2):33–35. https://doi.org/10.1046/j.1471-8278.2000.00013.x

Ash MM, Wolford KA, Carden TJ, Hwang KT, Carr TP (2011) Unrefined and refined black raspberry seed oils significantly lower triglycerides and moderately affect cholesterol metabolism in male Syrian hamsters. J Med Food 14(9):1032–1038. https://doi.org/10.1089/jmf.2010.0181

Barney DL, Fallahi E (2009) Growing currants, gooseberries & Jostaberries in the inland Northwest and intermountain West. University of Idaho Extension, Bul 855

Barney DL, Hummer KE (2005) Currants, gooseberries, and jostaberries: a guide for growers, marketers, and researchers in North America. CRC Press, Boca Raton

Basey A (2017) Grafted Blueberry Trial. http://oregonstate.edu/dept/NWREC/programs/berry-crops/grafted-blueberry-trial. Accessed 10/11/2017

Bassil NV, Davis TM, Zhang H, Ficklin S, Mittmann M, Webster L et al (2015) Development and preliminary evaluation of a 90K Axiom® SNP array for the allo-octoploid cultivated strawberry *Fragaria* × *ananassa*. BMC Genomics 16(155):30. https://doi.org/10.1186/s12864-015-1310-1

Bauer A (1986) New results of breeding *Ribes nidigrolaria*: Amphidiploid species hybrids between blackcurrant and gooseberry. Acta Hortic 183, 107–110. https://doi.org/10.17660/ActaHortic.1986.183.14

BGCI (2017) PlantSearch database. http://bgci.org/plant_search.php. Accessed 10 Aug 2017

Bian Y, Ballington J, Raja A, Brouwer C, Reid R, Burke M et al (2014) Patterns of simple sequence repeats in cultivated blueberries (Vaccinium section Cyanococcus spp.) and their use in revealing genetic diversity and population structure. Mol Breed 34(2):675–689

Bolda MP, Goodhue RE, Zalom FG (2010) Spotted wing drosophila: potential economic impact of a newly established pest. Giannini Found Agric Econ 13:5–8

Brazelton C, Young K (2017) World blueberry statistics and global market analysis. Paper presented at the International Blueberry Organization 2016

Brennan RM (1996) Currants and gooseberries. In: Janick J, Moore JN (eds) Fruit breeding, vol. 2: vine and small fruit crops. John Wiley & Sons, Inc., New York, pp 191–295

Brennan RM (2008) Currants and gooseberries. In: Temperate fruit crop breeding. Springer, New York, pp 177–196

Brennan RM, Jorgensen L, Woodhead M, Russell JR (2002) Development and characterization of SSR markers in Ribes species. Mol Ecol Notes 2(3):327–330. https://doi.org/10.1046/j.1471-8286.2002.00233.x

Brennan RM, Jorgensen L, Hackett C, Woodhead M, Gordon S, Russell JR (2008) The development of a genetic linkage map of blackcurrant (Ribes nigrum L.) and the identification of regions associated with key fruit quality and agronomic traits. Euphytica 161(1):19–34. https://doi.org/10.1007/s10681-007-9412-8

Brennan RM, Jorgensen L, Gordon S, Loades K, Hackett C, Russell JR (2009) The development of a PCR-based marker linked to resistance to the blackcurrant gall mite (Cecidophyopsis ribis Acari: Eriophyidae). Theor Appl Genet 118(2):205–211. https://doi.org/10.1007/s00122-008-0889-x

Bushakra JM, Stephens MJ, Atmadjaja AN, Lewers KS, Symonds VV, Udall JA et al (2012) Construction of black (*Rubus occidentalis*) and red (*R. idaeus*) raspberry linkage maps and their comparison to the genomes of strawberry, apple, and peach. Theor Appl Genet 125(2):311–327. https://doi.org/10.1007/s00122-012-1835-5

Bushakra JM, Bryant DW, Dossett M, Vining KJ, VanBuren R, Gilmore BS et al (2015) A genetic linkage map of black raspberry (*Rubus occidentalis*) and the mapping of Ag_4 conferring resistance to the aphid *Amphorophora agathonica*. Theor Appl Genet 128(8):1631–1646. https://doi.org/10.1007/s00122-015-2541-x

Caplan JS, Yeakley JA (2013) Functional morphology underlies performance differences among invasive and non-invasive ruderal Rubus species. Oecologia 173(2):363–374. https://doi.org/10.1007/s00442-013-2639-2

Castro-Lopez P, Stafne ET, Clark JR, Lewers KS (2013) Genetic map of the primocane-fruiting and thornless traits of tetraploid blackberry. Theor Appl Genet 126(10):2521–2532. https://doi.org/10.1007/s00122-013-2152-3

Cavanna M, Torello Marinoni D, Beccaro GL, Bounous G (2009) Microsatellite-based evaluation of Ribes spp. germplasm. Genome 52(10):839–848. https://doi.org/10.1139/G09-057

Chambers AH, Carle S, Njuguna W, Chamala S, Bassil NV, Whitaker VM et al (2013) A genome-enabled, high-throughput, and multiplexed fingerprinting platform for strawberry (*Fragaria* L.). Mol Breed 31:615–629. https://doi.org/10.1007/s11032-012-9819-3

Chambers AH, Pillet J, Plotto A, Bai J, Whitaker VM, Folta KM (2014) Identification of a strawberry flavor gene candidate using an integrated genetic-genomic-analytical chemistry approach. BMC Genomics 15(1):217

Clark JR, Finn CE (2011) Blackberry breeding and genetics. In: Flachowsky H, Hanke MV (eds) Methods in temperate fruit breeding. Fruit, vegetable and cereal science and biotechnology, vol 5. Global Science Books, Ltd, UK, Ikenobe, Japan. pp 27–43

Clark JR, Stafne ET, Hall HK, Finn CE (2007) Blackberry breeding and genetics. In: Janick J (ed) Plant breeding reviews, vol 29. John Wiley & Sons, Inc., New York, pp 19–144

Colquhoun TA, Levin LA, Moskowitz HR, Whitaker VM, Clark DG, Folta KM (2012) Framing the perfect strawberry: an exercise in consumer-assisted selection of fruit crops. J Berry Res 2(1):45–61

Compendium of Raspberry and Blackberry Diseases and Pests (2017) Martin RR, Ellis MA, Williamson B, Williams RN (eds) 2nd ed. APS Press, St. Paul

Covarrubias-Pazaran G, Diaz-Garcia L, Schlautman B, Deutsch J, Salazar W, Hernandez-Ochoa M et al (2016) Exploiting genotyping by sequencing to characterize the genomic structure of the American cranberry through high-density linkage mapping. BMC Genomics 17(1):451

Coville FV (1921) Directions for blueberry culture, 1921: US Department of Agriculture

Coville FV (1937) Improving the wild blueberry. US Department of Agriculture, Washington, DC

Darrow GM (1966) The strawberry. History, breeding and physiology

Daubeny HA (1996) Brambles. In: Janick J, Moore JN (eds) Fruit breeding, vol. II. Vine and small fruits. Wiley, New York, pp 109–190

Davis TM, Yu H (1997) A linkage map of the diploid strawberry, *Fragaria vesca*. J Hered 88(3):215–221

de Mattia F, Grassi F, Imazio S, Labra M (2008) Chloroplast and nuclear DNA markers to characterize cultivated and spontaneous Ribes. Plant Biosyst Int J Deal Asp Plant Biol 142(2):204–212. https://doi.org/10.1080/11263500802150290

Diekmann M, Frison E, Putter T (1994) FAO/IPGRI technical guidelines for the safe movement of small fruit germplasm, vol. 13. Bioversity International

Dossett M (2011) Evaluation of genetic diversity in wild populations of black raspberry (*Rubus occidentalis L.*) (Doctor of Philosophy), Oregon State University

Dossett M, Finn CE (2010) Identification of resistance to the large raspberry aphid in black raspberry. J Am Soc Hortic Sci 135(5):438–444

Dossett M, Kempler C (2012) Biotypic diversity and resistance to the raspberry aphid *Amphorophora agathonica* in Pacific Northwestern North America. J Am Soc Hortic Sci 137(6):445–451

Dossett M, Bassil NV, Finn CE (2012a) Fingerprinting of black raspberry cultivars shows discrepancies in identification. Acta Hort (ISHS) 946:49–53

Dossett M, Bassil NV, Lewers KS, Finn CE (2012b) Genetic diversity in wild and cultivated black raspberry (*Rubus occidentalis* L.) evaluated by simple sequence repeat markers. Genet Resour Crop Evol 59(8):1849–1865. https://doi.org/10.1007/s10722-012-9808-8

Duchesne AN (1766) Histoire Naturelle des Fraisiers. Didot le jeune, Paris

Eck P (1990) The American cranberry. Rutgers University Press, New Brunswick

Faedi W, Mourgues F, Rosati C (2000) Strawberry breeding and varieties: situation and perspectives. Paper presented at the IV International Strawberry Symposium 567

Fajardo D, Morales J, Zhu H, Steffan S, Harbut R, Bassil N et al (2013) Discrimination of American cranberry cultivars and assessment of clonal heterogeneity using microsatellite markers. Plant Mol Biol Report 31(2):264–271

Finn CE (2001) Trailing blackberries: from clear-cuts to your table. HortScience 36(2):236–238

Finn CE, Clark JR (2012) Blackberry. In: Badenes ML, Byrne DH (eds) *Fruit breeding*, vol 8. Springer, New York/Dordrecht/Heidelberg/London, pp 151–190

Garcia-Seco D, Zhang Y, Gutierrez-Manero F, Martin C, Ramos-Solano B (2015) RNA-Seq analysis and transcriptome assembly for blackberry (Rubus sp. Var. Lochness) fruit. BMC Genomics 16(1):5

Gaston A, Perrotte J, Lerceteau-Köhler E, Rousseau-Gueutin M, Petit A, Hernould M et al (2013) PFRU, a single dominant locus regulates the balance between sexual and asexual plant reproduction in cultivated strawberry. J Exp Bot 64:1837. https://doi.org/10.1093/jxb/ert047

Georgi L, Johnson-Cicalese J, Honig J, Das SP, Rajah VD, Bhattacharya D et al (2013) The first genetic map of the American cranberry: exploration of synteny conservation and quantitative trait loci. Theor Appl Genet 126(3):673–692

Global Crop Diversity Trust (2017) GENESYS. https://www.genesys-pgr.org/welcome. Accessed 18 Jan 2017

Gordon TR, Kirkpatrick SC, Henry PM, Kong M, Broome JC (2015) First report of a wilt disease of blackberry caused by *Fusarium oxysporum* in California. Plant Dis 100(5):1018–1018. https://doi.org/10.1094/PDIS-07-15-0784-PDN

Graham J, Smith K, MacKenzie K, Jorgenson L, Hackett C, Powell W (2004) The construction of a genetic linkage map of red raspberry (*Rubus idaeus* subsp. *idaeus*) based on AFLPs, genomic-SSR and EST-SSR markers. Theor Appl Genet 109(4):740–749

Gupta V, Estrada AD, Blakley I, Reid R, Patel K, Meyer MD et al (2015) RNA-Seq analysis and annotation of a draft blueberry genome assembly identifies candidate genes involved in fruit ripening, biosynthesis of bioactive compounds, and stage-specific alternative splicing. GigaScience 4(1):5

Hancock JF (2006a) California public strawberry breeders: a perfect marriage of genetics and culture. HortScience 41(1):16

Hancock JF (2006b) Highbush blueberry breeders. HortScience 41(1):20–21

Hancock JF, Lyrene P, Finn CE, Vorsa N, Lobos GA (2008a) Blueberries and Cranberries. In: Hancock JF (ed) Temperate fruit crop breeding: germplasm to genomics. Springer Netherlands, Dordrecht, pp 115–150

Hancock JF, Weebadde CK, Serçe S (2008b) Challenges faced by day-neutral strawberry breeders in the continental climates of the Eastern United States and Canada. HortScience 43(6):1635–1636

Hancock JF, Finn CE, Luby JJ, Dale A, Callow PW, Serçe S (2010) Reconstruction of the strawberry, *Fragaria* × *ananassa*, using genotypes of F. virginiana and F. chiloensis. HortScience 45(7):1006–1013

Harmat L, Porpaczy A, Himelrick D, Galletta G (1990) Currant and gooseberry management. In: Small fruit crop management. Prentice Hall, Englewood Cliffs, pp 245–272

Hokanson K, Smith M, Connor A, Luby J, Hancock JF (2006) Relationships among subspecies of New World octoploid strawberry species, Fragaria virginiana and Fragaria chiloensis, based on simple sequence repeat marker analysis. Botany 84(12):1829–1841

Howarth DG, Gardner DE, Morden CW (1997) Phylogeny of *Rubus* subgenus *Idaeobatus* (Rosaceae) and its implications toward colonization of the Hawaiian Islands. Syst Bot 22(3):433–441. https://doi.org/10.2307/2419819

Hummer KE (2008) Global conservation strategy for Fragaria (Strawberry). Scripta Hortic 6:87

Hummer KE, Dale A (2010) Horticulture of *Ribes*. For Pathol 40(3–4):251–263. https://doi.org/10.1111/j.1439-0329.2010.00657.x

Hummer KE, Bassil NV, Njuguna W (2011) Fragaria. In: Wild crop relatives: genomic and breeding resources. Springer, Heidelberg, pp 17–44

Hummer KE, Pomper KW, Postman JD, Graham CJ, Stover E, Mercure EW et al (2012) Emerging fruit crops. In: Fruit breeding. Springer, Boston, pp 97–147

ITPGRFA (2017) International treaty for plant genetic resources for food and agriculture. Retrieved 1/15/2017, from United Nations Food and Agriculture Organization http://www.fao.org/plant-treaty/en/

Jenderek MM, Forsline P, Postman J, Stover E, Ellis D (2011) Effect of geographical location, year and cultivar on survival of Malus sp. dormant buds stored in vapor of liquid nitrogen. Hortscience 46(9):1230–1234

Jennings DL (1988) Raspberries and blackberries: their breeding, diseases and growth. Academic Press, San Diego, CA

Jennings, H.A. Daubeny, J.N. Moore1991. Blackberries and raspberries (Rubus) J.N. Moore, J.R. Ballington Jr. (Eds.), Genetic Resources of Temperate Fruit and Nut Crops, Volume 1, ISHS, Wageningen, The Netherlands (1991), p. 355

Koskela EA, Sønsteby A, Flachowsky H, Heide OM, Hanke MV, Elomaa P, Hytönen T (2016) TERMINAL FLOWER1 is a breeding target for a novel everbearing trait and tailored flowering responses in cultivated strawberry (*Fragaria* × *ananassa* Duch.). Plant Biotechnol J 14:1852–1861

Kron KA, Powell EA, Luteyn JL (2002) Phylogenetic relationships within the blueberry tribe (Vaccinieae, Ericaceae) based on sequence data from *MATK* and nuclear ribosomal ITS regions, with comments on the placement of *Satyria*. Am J Bot 89(2):327–336. https://doi.org/10.3732/ajb.89.2.327

Lee V (1964) Antoine Nicolas Duchesne—First strawberry hybridist. Am Hortic Mag 43:80–88

Lerceteau-Köhler E, Moing A, Guérin G, Renaud C, Petit A, Rothan C, Denoyes B (2012) Genetic dissection of fruit quality traits in the octoploid cultivated strawberry highlights the role of homoeo-QTL in their control. Theor Appl Genet 124(6):1059–1077

Lewers KS, Saski C, Cuthbertson B, Henry D, Staton M, Main D et al (2008) A blackberry (*Rubus* L.) expressed sequence tag library for the development of simple sequence repeat markers. BMC Plant Biol 8(1):69

Liston A, Cronn R, Ashman T-L (2014) Fragaria: a genus with deep historical roots and ripe for evolutionary and ecological insights. Am J Bot 101(10):1686–1699

Maas JL (1998) Compendium of strawberry diseases, 2nd edn. APS Press, St. Paul, pp 1–98

Mace TA, King SA, Ameen Z, Elnaggar O, Young G, Riedl KM et al (2014) Bioactive compounds or metabolites from black raspberries modulate T lymphocyte proliferation, myeloid cell differentiation and Jak/STAT signaling. Cancer Immunol Immunother 63(9):889–900. https://doi.org/10.1007/s00262-014-1564-5

Martin RR, Polashock JJ, Tzanetakis IE (2012) New and emerging viruses of blueberry and cranberry. Viruses 4(11):2831–2852. https://doi.org/10.3390/v4112831

McCallum S, Graham J, Jorgensen L, Rowland LJ, Bassil NV, Hancock JF et al (2016) Construction of a SNP and SSR linkage map in autotetraploid blueberry using genotyping by sequencing. Mol Breed 36(4):1–24

Moerman DE (1996) An analysis of the food plants and drug plants of native North America. J Ethnopharmacol 52(1):1–22. https://doi.org/10.1016/0378-8741(96)01393-1

Moerman DE (2009) Native American medicinal plants: an ethnobotanical dictionary. Timber Press, Portland

Montrose DC, Horelik NA, Madigan JP, Stoner GD, Wang L-S, Bruno RS et al (2011) Anti-inflammatory effects of freeze-dried black raspberry powder in ulcerative colitis. Carcinogenesis 32(3):343–350. https://doi.org/10.1093/carcin/bgq248

Morden CW, Gardner DE, Weniger DA (2003) Phylogeny and biogeography of Pacific *Rubus* subgenus *Idaeobatus* (Rosaceae) species: investigating the origin of the endemic Hawaiian raspberry *R. macraei*. Pac Sci 57(2):181–197

Mortaş H, Şanlıer N (2017) Nutritional evaluation of commonly consumed berries: composition and health effects. Fruits 72(1):5–23. https://doi.org/10.17660/th2017/72.1.1

Moyer RA, Hummer KE, Finn CE, Frei B, Wrolstad RE (2002) Anthocyanins, phenolics, and antioxidant capacity in diverse small fruits: *Vaccinium*, *Rubus*, and *Ribes*. J Agric Food Chem 50(3):519–525. https://doi.org/10.1021/jf011062r

NatureServe (2017) NatureServe Explorer: an online encyclopedia of life [web application]. Version 7.1. From NatureServe http://explorer.natureserve.org

Neto CC, Amoroso JW, Liberty AM (2008) Anticancer activities of cranberry phytochemicals: An update. Mol Nutr Food Res 52(S1), S18–S27. https://doi.org/10.1002/mnfr.200700433

Polashock J, Zelzion E, Fajardo D, Zalapa J, Georgi L, Bhattacharya D, Vorsa N (2014) The American cranberry: first insights into the whole genome of a species adapted to bog habitat. BMC Plant Biol 14(1):165

Postman JD, Hummer KE, Stover E, Krueger R, Forsline P, Grauke LJ et al (2006) Fruit and nut genebanks in the U.S. National Plant Germplasm System. *HortScience* 41(5):1188–1194

Richardson CW (1914) A preliminary note on the genetics of *Fragaria*. J Genet 3(3):171–177. https://doi.org/10.1007/bf02981712

Rodrigo KA, Rawal Y, Renner RJ, Schwartz SJ, Tian Q, Larsen PE, Mallery SR (2006) Suppression of the tumorigenic phenotype in human oral squamous cell carcinoma cells by an ethanol extract derived from freeze-dried black raspberries. Nutr Cancer 54(1):58–68. https://doi.org/10.1207/s15327914nc5401_7

Rowland LJ, Ogden EL, Bassil N, Buck EJ, McCallum S, Graham J et al (2014) Construction of a genetic linkage map of an interspecific diploid blueberry population and identification of QTL for chilling requirement and cold hardiness. Mol Breed 34(4):2033–2048

Russell JR, Bayer M, Booth C, Cardle L, Hackett CA, Hedley PE et al (2011) Identification, utilisation and mapping of novel transcriptome-based markers from blackcurrant (Ribes nigrum). BMC Plant Biol 11(1):147. https://doi.org/10.1186/1471-2229-11-147

Russell JR, Hackett C, Hedley P, Liu H, Milne L, Bayer M et al (2014) The use of genotyping by sequencing in blackcurrant (Ribes nigrum): developing high-resolution linkage maps in species without reference genome sequences. Mol Breed 33(4):835–849. https://doi.org/10.1007/s11032-013-9996-8

Salentijn EM, Aharoni A, Schaart JG, Boone MJ, Krens FA (2003) Differential gene expression analysis of strawberry cultivars that differ in fruit-firmness. Physiol Plant 118(4):571–578

Sargent DJ, Davis TM, Tobutt KR, Wilkinson MJ, Battey NH, Simpson DW (2004) A genetic linkage map of microsatellite, gene-specific and morphological markers in diploid *Fragaria*. Theor Appl Genet 109(7):1385–1391

Sargent DJ, Clarke J, Simpson DW, Tobutt KR, Arús P, Monfort A et al (2006) An enhanced microsatellite map of diploid *Fragaria*. Theor Appl Genet 112(7):1349–1359

Sargent DJ, Fernández-Fernández F, Rys A, Knight V, Simpson DW, Tobutt KR (2007) Mapping of *A1* conferring resistance to the aphid *Amphorophora idaei* and *dw* (dwarfing habit) in red raspberry (*Rubus idaeus* L.) using AFLP and microsatellite markers. BMC Plant Biol 7(1):15

Scheerens JC, Erb WA, Goulart BL, Hancock JF (1999a) Blueberry hybrids with complex genetic backgrounds evaluated on mineral soils: flowering, fruit development, yield and yield components as influenced by parental species. Fruit Varieties J 53:91–104

Scheerens JC, Erb WA, Goulart BL, Hancock JF (1999b) Blueberry hybrids with complex genetic backgrounds evaluated on mineral soils: stature, growth rate, yield potential and adaptability to mineral soil conditions as influenced by parental species. Fruit Varieties J 53:73–90

Schlautman B, Fajardo D, Bougie T, Wiesman E, Polashock J, Vorsa N et al (2015) Development and validation of 697 novel polymorphic genomic and EST-SSR markers in the American cranberry (Vaccinium macrocarpon Ait.). Molecules 20(2):2001–2013

Schwab W, Schaart JG, Rosati C (2009) Functional molecular biology research in Fragaria. In: Genetics and genomics of Rosaceae. Springer, New York, pp 457–486

Shulaev V, Sargent DJ, Crowhurst RN, Mockler TC, Folkerts O, Delcher AL et al (2011) The genome of woodland strawberry (*Fragaria vesca*). Nat Genet 43(2):109–116. http://www.nature.com/ng/journal/v43/n2/abs/ng.740.html#supplementary-information

Sjulin TM (2006) Private strawberry breeders in California. HortScience 41(1):17–19

Song G-Q, Hancock JF (2011) Vaccinium. In: Wild crop relatives: Genomic and breeding resources. Springer Nature Switzerland AG, pp 197–221

Staudt G (1962) Taxonomic studies in the genus Fragaria typification of Fragaria species known at the time of Linnaeus. Can J Bot 40(6):869–886

Staudt G (1999) Systematics and geographic distribution of the American strawberry species: taxonomic studies in the genus Fragaria (Rosaceae: Potentilleae), Univ Calif Berkeley Publ Bot 81:125

Staudt G (2009) Strawberry biogeography, genetics and systematics. Acta Hortic 842:71–84. https://doi.org/10.17660/ActaHortic.2009.842.1

Stegmeir TL, Finn CE, Warner RM, Hancock JF (2010) Performance of an elite strawberry population derived from wild germplasm of Fragaria chiloensis and F. virginiana. HortScience 45(8):1140–1145

Stevens M, Darris DC (2003) Plant guide: Salmonberry. In: USDA-NRCS (ed), vol. 060809 jsp

Stoner GD, Sardo C, Apseloff G, Mullet D, Wargo W, Pound V et al (2005) Pharmacokinetics of anthocyanins and ellagic acid in healthy volunteers fed freeze-dried black raspberries daily for 7 days. J Clin Pharmacol 45(10):1153–1164. https://doi.org/10.1177/0091270005279636

Stoner GD, Wang L-S, Zikri N, Chen T, Hecht SS, Huang C et al (2007) Cancer prevention with freeze-dried berries and berry components. Semin Cancer Biol 17(5):403–410. https://doi.org/10.1016/j.semcancer.2007.05.001

Strik BC, Clark JR, Finn CE, Bañados MP (2007) Worldwide blackberry production. HortTechnology 17(2):205–213

Thompson MM (1995) Chromosome numbers of *Rubus* species at the National Clonal Germplasm Repository. HortScience 30(7):1447–1452

UNFAO. (2017). United Nations Food and Agriculture Organization. Retrieved 02/04/2017 http://www.fao.org/faostat/en/#data/QC

US Fish & Wildlife Service, Environmental Conservation Online System (2015) Ribes echinellum (Miccosukee gooseberry) 5-year review: summary and evaluation. Accessed from https://ecos.fws.gov/ecp0/profile/speciesProfile.action?spcode=Q217

USDA, ARS, National Plant Germplasm System (2017a) Germplasm Resources Information Network (GRIN Global) database. National Germplasm Resources Laboratory, Beltsville, MD. https://www.ars-grin.gov/npgs/acc/acc_queries.html. Accessed 14 Jan 2017

USDA, ARS, National Plant Germplasm System (2017b) Germplasm Resources Information Network (GRIN Global) Taxonomy. National Germplasm Resources Laboratory, Beltsville, MD. https://npgsweb.ars-grin.gov/gringlobal/taxon/taxonomyquery.aspx. Accessed 27 Sept 2017

USDA-ERS (2010) Economic Research Service. Retrieved 01/15/2017 https://www.ers.usda.gov/topics/crops/fruit-tree-nuts/data.aspx

USDA-ERS (2018) U.S. Department of Agriculture, Economic Research Service. Fruit and Tree Nut Yearbook Tables. Available at: https://www.ers.usda.gov/data-products/fruit-and-tree-nut-data/fruit-and-tree-nut-yearbook-tables/. Accessed November 2018.

USDA-NASS (2015) National Agricultural Statistics Service. Retrieved 01/15/2017 https://nassgeodata.gmu.edu/CropScape/

USDA-NDL (2017) Nutrient Data Library. Retrieved 02/14/2017 https://www.ars.usda.gov/northeast-area/beltsville-md/beltsville-human-nutrition-research-center/nutrient-data-laboratory/

USDA-NRCS (2017) Natural Resource Conservation Service. https://plants.usda.gov/java/threat

van Dijk T, Pagliarani G, Pikunova A, Noordijk Y, Yilmaz-Temel H, Meulenbroek B et al (2014) Genomic rearrangements and signatures of breeding in the allo-octoploid strawberry as revealed through an allele dose based SSR linkage map. BMC Plant Biol 14(1):55

VanBuren R, Bryant D, Bushakra JM, Vining KJ, Edger PP, Rowley ER et al (2016) The genome of black raspberry (*Rubus occidentalis*). Plant J 87(6):535–547. https://doi.org/10.1111/tpj.13215

Vander Kloet SP (2004) Vaccinia gloriosa. Small Fruits Rev 3(3–4):221–227. https://doi.org/10.1300/J301v03n03_01

Ward JA, Bhangoo J, Fernández-Fernández F, Moore PP, Swanson JD, Viola R et al (2013) Saturated linkage map construction in *Rubus idaeus* using genotyping by sequencing and genome-independent imputation. BMC Genomics 14(1):2

Weber CA (2003) Genetic diversity in black raspberry detected by RAPD markers. HortScience 38(2):269–272

Weber CA (2013) Cultivar development and selection. In: Funt RC, Hall HK (eds) Raspberries. CAB International, London, pp 55–72

Wiersema JH, León B (2016) World economic plants: a standard reference. CRC Press, Boca Raton

Wilhelm S, Sagen JE (1974) A history of the strawberry: from ancient gardens to modern markets. University of California, Division of Agricultural Sciences, Berkeley

Woodhead M, Weir A, Smith K, McCallum S, MacKenzie K, Graham J (2010) Functional markers for red raspberry. J Am Soc Hortic Sci 135(5):418–427

Woodward M (1924) Gerard's herball. The essence thereof distilled by Marcus Woodward from the edition of Thomas Johnson. Gerald Howe, London, p 1636

Zhang Z, Knobloch TJ, Seamon LG, Stoner GD, Cohn DE, Paskett ED et al (2011) A black raspberry extract inhibits proliferation and regulates apoptosis in cervical cancer cells. Gynecol Oncol 123(2):401–406. https://doi.org/10.1016/j.ygyno.2011.07.023

Zikri NN, Riedl KM, Wang L-S, Lechner J, Schwartz SJ, Stoner GD (2009) Black raspberry components inhibit proliferation, induce apoptosis, and modulate gene expression in rat esophageal epithelial cells. Nutr Cancer 61(6):816–826. https://doi.org/10.1080/01635580903285148

Zorrilla-Fontanesi Y, Cabeza A, Torres A, Botella M, Valpuesta V, Monfort A et al (2011) Development and bin mapping of strawberry genic-SSRs in diploid *Fragaria* and their transferability across the Rosoideae subfamily. Mol Breed 27(2):137–156. https://doi.org/10.1007/s11032-010-9417-1