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Abstract	<p>The Rosaceae family consists of around 3,000 species of which 500 belong to the genus <i>Rubus</i>. Ploidy levels range from diploid to dodecaploid with a genomic number of 7, and members can be difficult to classify into distinct species due to hybridization and apomixes. Species are distributed widely across Asia, Europe, and North and South America, with the center of diversity now considered to be in China, where there are 250–700 species of <i>Rubus</i> depending on the taxonomists. <i>Rubus</i> species are an important horticultural source of income and labor being produced for the fresh and processing markets for their health benefits. Blackberries and raspberries have a relatively short history of less than a century as cultivated crops that have been enhanced through plant breeding and they are only a few generations removed from their wild progenitor species. <i>Rubus</i> species are typically found as early colonizers of disturbed sites such as pastures, along forest edges, in forest clearings, and along roadsides. Blackberries are typically much more tolerant of drought, flooding, and high temperatures, while red raspberries are more tolerant of cold winters. Additionally, they exhibit vigorous vegetative reproduction by either tip layering or root suckering, permitting <i>Rubus</i> genotypes to cover large areas. The attractiveness of the fruits to frugivores, especially birds, means that seed dispersal can be widespread with the result that <i>Rubus</i> genotypes can very easily be spread to new sites and are very effective, high-speed invaders. Nevertheless, wild <i>Rubus</i> species represent a valuable genetic resource, and protecting this biodiversity for future <i>Rubus</i> breeding programs is essential as breeders respond to changes in environmental and growing conditions.</p>
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Chapter 9

Rubus

J. Graham and M. Woodhead

9.1 Basic Botany of the Species

The genus *Rubus* is composed of a highly heterozygous series of some 500 species, with a range of ploidy levels from diploid to duodecaploid (Jennings 1988; Meng and Finn 2002). Hundreds of species are divided botanically under 15 subgenera, many of which have been used in breeding (Jennings et al. 1991; Knight 1993; Finn 2001; Finn and Knight 2002; Finn et al. 2002). Members of the genus can be difficult to classify into distinct species for a number of reasons, including hybridization between species and apomixes (Robertson 1974; Dickinson et al. 2007; Evans et al. 2007). Cytological data are being generated and used in an attempt to gain insight into the relationships of the genus (Wang et al. 2008). The subgenus *Rubus* is divided into 12 sections with most of the cultivated blackberries being derived from the *Allegheniensis*, *Arguti*, *Flagellares*, *Rubus*, *Ursini*, and/or *Verotrivialis* (Gustafsson 1943; Finn 2008). Red and black raspberries along with many of the wild harvested species from around the world are in the *Idaeobatus* subgenus.

Commercially, the most important raspberries are the European red raspberry, *R. idaeus* L. subsp. *idaeus*, the North American red raspberry *R. idaeus* subsp. *strigosus* Michx, and the black raspberry (*Rubus occidentalis* L.). *Rubus* subgen. *Idaeobatus* is distributed principally in Asia as well as in East and South Africa, Europe, and North America. In contrast, subgen. *Eubatus* is mainly distributed in South America, Europe, and North America (Jennings 1988). The members

of subgenus *Idaeobatus* sp. are distinguished by the ability of their mature fruits to separate from the receptacle. The subgenus is particularly well represented in the northern Hemisphere. The place of origin of raspberry has been postulated to be the Ide Mountains of Turkey (Jennings 1988). The center of diversity is considered to be in China, where there are 250–700 species of *Rubus* depending on the taxonomists (Thompson 1997). Jennings (1988) and Roach (1985) have given extensive accounts of early domestication. Records were found in the fourth century writings of Palladius, a Roman agriculturist, and seeds have been discovered at Roman forts in Britain; hence, the Romans probably spread cultivation throughout Europe.

Rubus species are prostrate to erect, generally thorny shrubs producing renewal shoots from the ground (called canes). They are perennials only because each bush consists of biennial canes, which overlap in age. Leaves are compound with 3–5 leaflets, the middle one being the largest; margins serrate to irregularly toothed. Small (0.5–1.5 cm), white to pink flowers are initiated in the second year of planting. The gynoecium consists of 60–80 ovaries, each of which develops into a drupelet. There are 60–90 stamens. The flowers of *Rubus* are structurally rather similar to those of strawberries, with five sepals, five petals, a very short hypanthium, many stamens, and an apocarpous gynoecium of many carpels on a cone-like receptacle. They produce an aggregate fruit, composed of individual drupelets, held together by almost invisible hairs. In *Rubus*, each carpel will develop into a small drupelet, with the mesocarp becoming fleshy and the endocarp becoming hard and forming a tiny pit that encloses a single seed. Each drupelet usually has a single seed, though a few have two. Canes grow 1 year and fruit the next, but there are also primocane

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72 varieties, which fruit in the first year. The biennial
73 growth cycle of stems begins when a bud from below
74 soil level develops and elongation of the internodes
75 carries the growing point, protected by leaf scales, to
76 the soil surface. At the surface, leaves expand to form
77 a tight rosette around the growing point. Elongation of
78 the shoot starts in spring and continues until autumn,
79 by which time the shoot will have attained a height of
80 2–3 m. In red raspberries (*R. idaeus* L.), shortening
81 days and falling temperatures in late summer cause
82 shoot elongation to cease and dormancy to set in. This
83 is a gradual process extending over several weeks, and
84 once a stage of complete dormancy is reached, it is not
85 readily reversible. Black raspberries (*R. occidentalis* L.)
86 or purple raspberries (hybrids between red and black
87 raspberries) and most blackberries differ from red
88 raspberries both in time when dormancy begins and
89 intensity of dormancy attained. In these fruits, growth
90 continues well into autumn. The initiation of flower
91 buds usually starts at the same time as the canes begin
92 to acquire dormancy. In the spring of the second year,
93 vegetative primocanes become fruiting canes. The
94 fruit is composed of a large number of one-seeded
95 drupelets set together on a small conical core
96 (Jennings 1988). Commercial blackberries are classi-
97 fied into three categories based on cane type: trailing,
98 semi-erect, and erect (Strik 1992). Trailing types and
99 semi-erect habit blackberries are crown-forming,
100 and the primocanes trail on the ground surface until
101 lifted and staked. Erect blackberries grow upright
102 but less vigorously than the semi-erect types, and
103 instead of being crown-forming, they sucker beneath
104 the soil line.

105 The genomic number of *Rubus* is seven and species
106 representing all ploidies from diploid to duodecaploid
107 are found in nature. The range in size is from 1 to 4 μm
108 (Jennings 1988). The diploid genome has been esti-
109 mated to be 275 Mbp. Self-incompatibility systems
110 occur in some Rosaceous species and are common
111 among many of the diploid *Rubus* species (Keep
112 1968). In contrast, all polyploid species are self-com-
113 patible as are the domesticated forms of the diploid
114 raspberries.

115 *Rubus* species are an important horticultural source
116 of income and labor. In most countries, fruit from
117 *Rubus* species is produced for the fresh market. Fruit
118 for processing is usually used in the food and beverage
119 industries where it is used to produce wine, beer, soft
120 drinks, preserves, and desserts. Fruits may also be

121 frozen or canned. Blackberry production is rapidly
122 increasing (Strik 1992; Clark 2005; Clark et al. 2007;
123 Strik et al. 2007) with an estimated 140,292 MT com-
124 mercially harvested from 20,035 ha in 2005. Europe
125 leads in the world in acreage (7,692 ha), while North
126 America has the highest production (59,123 MT).
127 Serbia (69%) dominates European production; how-
128 ever, a number of countries have significant produc-
129 tion. In North America, the US, particularly the
130 Oregon State, is the major producer. However, Mexican
131 production has been rapidly increasing. California and
132 Arkansas are the only other states in the US with over
133 1,000 MT production. Central American production
134 (1,620 ha) is predominantly from Costa Rica and Gua-
135 temala where in addition to harvest from managed
136 stands, a great deal is harvested from feral stands.
137 South American production (1,597 ha) is predomi-
138 nantly from Ecuador and Chile. Asian production has
139 been rapidly increasing with over 1,550 ha of new
140 plantings, predominantly in China. The production in
141 Oceania is mainly in New Zealand, although the area
142 planted is small with only about 259 ha. African pro-
143 duction is only reported in South Africa but has been
144 initiated in Morocco, Algeria, Kenya, and possibly
145 others. The bulk of the fruit is grown for processing
146 applications in the Pacific Northwest US, Serbia, and
147 China, whereas fresh market sales are the focus of the
148 industry elsewhere.

149 Raspberry is an important high-value horticultural
150 industry in many parts of the world, providing
151 employment directly in agriculture and indirectly in
152 food processing and confectionary. Production is
153 estimated at 482,763 MT (2005) (<http://FAOSTAT.FAO.ORG>). Europe is estimated to produce around
154 half of all production of *Rubus idaeus* L. Most rasp-
155 berry production is concentrated in the northern and
156 central European countries, although there is an
157 increasing interest in growing cane fruits in southern
158 Europe, e.g., in Greece, Italy, Portugal, and Spain.
159 The major production areas of red raspberries in
160 North America are the Pacific Northwest (Oregon,
161 Washington, and British Columbia), California, the
162 eastern US (New York, Michigan, Pennsylvania, and
163 Ohio), and a rapidly expanding industry in Mexico.
164 While adapted to many of the same areas as the other
165 cultivated *Rubus*, black raspberry (*R. occidentalis*)
166 cultivation is concentrated in Oregon in the western
167 US, in Ohio, Pennsylvania and New York in the
168 eastern US, and in Korea. 169

170 **9.2 Conservation Initiatives**

171 A number of studies have been carried out to charac-
172 terize the levels of genetic variation in wild species
173 and to examine the turnover of wild populations. In the
174 Tayside region of Scotland, a study of wild raspberry
175 populations had been carried out over a 10-year
176 period. Initially, Graham et al. (1997) examined the
177 spatial genetic diversity in wild accessions of red
178 raspberry from four sites. Most of the variability
179 detected using random amplified polymorphic DNA
180 (RAPD) markers was observed between the collection
181 sites. Within sites, increasing diversity coincided with
182 greater spatial separation. None of the wild popula-
183 tions were closely related to any of the commonly
184 grown commercial cultivars and were all spiny.
185 A larger study examined a wider range of wild
186 *R. idaeus* from 12 sites across a greater area and
187 compared the accessions to the cultivar “Glen Moy.”
188 Again, greater genetic similarity was found within
189 each population collected, which indicates a hindrance
190 to gene movement across geographic locations. This
191 barrier to gene flow was partly explained by a separa-
192 tion of flowering period, with altitude proving to be
193 important here (Graham et al. 2003). Marshall et al.
194 (2001) examined some of the wild accessions studied
195 by Graham et al. (1997) to determine whether these
196 populations were adaptively differentiated from each
197 other. Plants were brought into a common environ-
198 ment and 20 traits assessed. A consistent north–south
199 trend was identified confirming substantive differenti-
200 ation between populations. Similar studies using phe-
201 notypic characteristics have been carried out on 12
202 wild raspberry populations in Russia (Ryabova
203 2007), where wild populations were examined for
204 characteristics, which may be useful in cultivated rasp-
205 berries. Ten years after these initial Scottish studies
206 had been carried out, these wild red raspberry plants at
207 12 sites were reexamined for changes in population
208 size and to address an earlier finding, which demon-
209 strated significant population differentiation over a
210 small scale (Graham et al. 2009a). Reductions in
211 plant numbers was observed at almost all sites.
212 Given that each population had unique alleles, which
213 could be identified even in a small number of plants,
214 this loss of plants also equates to a loss of alleles. The
215 studies of Marshall et al. (2001) reinforce the value of
216 this wild germplasm having demonstrated plants from

these locations (spanning an altitudinal cline from 5 to 217
600 m) exhibit significant variation in flowering and 218
fruiting period in a common environment. In the light 219
of current climate change implications, these popula- 220
tions represent a huge genetic resource that could be 221
utilized within commercial red raspberry breeding 222
programs to develop new cultivars better adapted to 223
a changing natural environment. 224

R. idaeus wild accessions from a Lithuanian germ- 225
plasm collection were examined for genetic diversity 226
using RAPD loci (Patamsytė et al. 2004). Soil acidity 227
rather than geographic distance was significantly cor- 228
related to observed polymorphisms, indicating an 229
environmental effect on diversity within populations. 230
DNA probes from two variable number tandem repeat 231
(VNTR) loci were utilized to examine diversity in wild 232
populations of *R. moluccanus* L. in the Philippines 233
(Busemeyer et al. 1997). The results were similar to 234
that of Graham et al. (1997, 2003), finding greater 235
similarity present within populations at each location 236
than between locations. Additionally, apomictic repro- 237
duction was ruled out in these populations because no 238
identical VNTR patterns were identified. 239

Research on natural populations of arctic raspberry 240
has shown genetic diversity at levels near 50% for 241
among and within population estimates (e.g., Lindqvist- 242
Kreuze et al. 2003). Genetic diversity has been 243
examined in natural populations of black raspberry 244
(*R. coreanus*) in Korea using inter simple sequence 245
repeat (ISSR) markers (Hong et al. 2003), and overall 246
genetic relationships among populations were asso- 247
ciated with geographic location. Black raspberry 248
(*R. leucodermis*) populations have also been evaluated 249
for traits of importance for use in red and black rasp- 250
berry breeding (Finn et al. 2003). A study on 63 251
natural populations of *Rubus strigosus* across North 252
America (Marking 2006) using chloroplast sequence 253
and ISSR found the majority of the variation to be 254
within populations (79.5%). 255

Cloudberry (*Rubus chamaemorus*) is a highly val- 256
ued berry in Scandinavia and northern Russia and has 257
potential for domestication (Korpelainen et al. 1999). 258
It reproduces primarily through clonal growth (Makinen 259
and Oikarinen 1974) and although sexual reproduction 260
occurs rarely, this is obviously important for coloniz- 261
ing new habitats. *R. chamaemorus* exhibits large mor- 262
phological differences, but genetic studies on Finnish 263
populations indicate that the levels of genetic diversity 264

265 within populations were quite low, comprising 2–4
 266 clonal genotypes per population (Korpelainen et al.
 267 1999). This has implications for domestication and
 268 breeding programs because the clear morphological
 269 variability observed may be largely influenced by
 270 environmental conditions. Therefore, plants for breed-
 271 ing programs should be selected from populations
 272 located some significant distance apart (Korpelainen
 273 et al. 1999).

274 A number of formal and informal gene bank collec-
 275 tions exist around the world. These include a *Rubus*
 276 collection of over 140 species and 302 named cultivars
 277 and selections with seed or clones available on
 278 request, housed in the USDA-ARS National Clonal
 279 Germplasm Repository (Hummer and Finn 1999).
 280 Another *Rubus* collection of over 140 accessions is
 281 maintained in a field collection and in protected cul-
 282 ture at the Canadian Clonal Genebank (Luffman
 283 1993). A gene bank inventory is published annually.
 284 In the UK field, collections of over 150 accessions
 285 exist at SCRI in Scotland and at East Malling Research
 286 in England (A. Dolan personal communication). Col-
 287 lections resulting from botanical surveys in Columbia
 288 consist of ten *Rubus* species recorded in open and/or
 289 disturbed habitats (Rivera et al. 1997). Plant material
 290 and seeds from exploration trips in Sakhalin territory
 291 are stored in gene banks including an orange *R. cha-*
 292 *maemorus* and a dark purple cloudberry (*R. pseudo-*
 293 *chamaemorus*) (Sabitov et al. 2007). Genotypes from
 294 seven Chinese provinces have been established in
 295 Jiangsu province and evaluated for a range of charac-
 296 teristics (Yin et al. 1996).

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296 In Europe, efforts are being made to conserve the
 297 biodiversity of berries (Bartha-Pichler 2006) with an
 298 interest in the conservation of genetic resources. The
 299 “GENBERRY” project, partly funded by the European
 300 Community, has been designed to ensure that agricul-
 301 tural biodiversity of small berries is preserved, char-
 302 acterized, and used to improve varieties adapted
 303 to local European regions. Strawberry (*Fragaria* ×
 304 *ananassa*) and raspberry (*R. idaeus*) represent the
 305 two main cultivated small berries. The project is
 306 focusing on the construction of core collections, the
 307 development of a passport data list, the selection and
 308 definition of appropriate primary and secondary
 309 descriptors, characterization of genotypes using
 310 molecular markers, identification of health nutritional
 311 compounds and diseases evaluation for a large subset of
 312 the collections, and the establishment of the European

small berries database sustained by a continuous long
 term network (Denoyes-Rothan et al. 2008). Roma-
 nian (Rusu et al. 2006a) and Bulgarian red raspberries
 (Badjakov et al. 2006) have been studied to determine
 their similarity with European and American germ-
 plasm using simple sequence repeat (SSR) markers.
 Badjakov et al. (2006) analyzed 28 raspberry geno-
 types from the Bulgarian germplasm collection includ-
 ing 18 Bulgarian cultivars and breeding lines, eight
 accessions from outside Bulgaria, and two wild spe-
 cies accessions, *R. occidentalis* and *R. adiene*, using
 RAPD markers. They created a genetic similarity tree
 with two clusters, which corresponded to two pedigree
 groups among the Bulgarian genotypes. They also
 analyzed the 28 accessions with four SSR loci, demon-
 strating high levels of diversity within the collection
 (Badjakov et al. 2006). Weber (2003) analyzed genetic
 diversity in cultivars of black raspberry (*R. occidenta-*
lis) and red raspberry using RAPD markers and found
 that black raspberry genotypes showed on an average
 81% genetic similarity. This compared well to the
 70% similarity measured among red raspberry culti-
 vars in Europe (Graham et al. 1994). Of the 16 geno-
 types investigated, five cultivars accounted for 58% of
 the observed variability in black raspberry, and none
 of the black raspberry cultivars were more than two
 generations from at least one wild ancestor.

9.3 Role in Elucidation of Origin and Evolution of Allied Crop Plants

Blackberries and raspberries have a relatively short
 history of less than a century as cultivated crops that
 have been enhanced through plant breeding and they
 are only a few generations removed from their wild
 progenitor species. The improvements that have
 allowed these plants to be commercial cultivated
 crops are well documented: including increased
 yield, improved harvest efficiency, abiotic and biotic
 stress tolerance, increased fruit quality for fresh and
 processed markets, altered plant architecture, etc.
 Roach (1985) and Jennings (1988) gave accounts of
 the early domestication of red raspberry (*R. idaeus* L.).
 During the nineteenth century, the North American red
 raspberry (*R. idaeus* subsp. *strigosus* Michx) was intro-
 duced into Europe and subsequently crossed with the
 European subspecies (*R. idaeus* subsp. *vulgatus*

358 Arrhen.). Five parent cultivars dominate the ancestry
 359 of red raspberry; “Lloyd George” and “Pynes Royal”
 360 entirely derived from *R. idaeus* var. *vulgatus*, and
 361 “Preussen,” “Cuthbert,” and “Newburgh” derived
 362 from both subspecies. Controlled crossing began
 363 slightly earlier in the US than in the UK with the
 364 introduction of “Latham” in 1914 (McNicol and
 365 Graham 1992). There are many excellent reviews on
 366 blackberry and raspberry breeding, genetics, and
 367 germplasm including (Darrow 1937; Daubeny 1996;
 368 Waldo 1968; Oydvin 1970; Sherman and Sharpe 1971;
 369 Jennings 1988; Hall 1990; Jennings et al. 1991; Moore
 370 1984; Clark and Finn 2008).

371 The development and application of molecular
 372 markers has allowed improvements in taxonomical
 373 classification to be made as well as providing tools
 374 for the development of genetic linkage mapping, fin-
 375 gerprinting, and assessments of diversity to be under-
 376 taken in raspberry. Marker development has been
 377 reviewed by Antonius-Klemola (1999), Hokanson
 378 (2001) and Skirvin et al. (2005). As well as the deploy-
 379 ment of anonymous DNA markers such as RAPDs
 380 (Graham et al. 1994, 1997; Weber 2003) and amplified
 381 fragment length polymorphisms (AFLPs) (Graham
 382 et al. 2006), SSR, EST-SSR, and single nucleotide
 383 polymorphism (SNP) markers have been developed
 384 (Graham et al. 2002, 2004, 2006; Stafne et al. 2005;
 385 Lewers et al. 2005; Lopes et al. 2006; Woodhead et al.
 386 2008; McCallum et al. 2010) and can be used to
 387 characterize *Rubus* accessions.

388 Alice and Campbell (1999) produced a *Rubus* phy-
 389 logeny of 57 species including multiple raspberry spe-
 390 cies based on ribosomal internal transcribed spacer
 391 region (ITSR) sequence variation. The *Rubus* subge-
 392 nus *Idaeobatus* of the Pacific region was studied in
 393 comparison with species from other subgenera to eval-
 394 uate biogeographic and phylogenetic affinities of
 395 *R. macraei*, using chromosome analysis and chloro-
 396 plast gene *ndhF* sequence (Morden et al. 2003). Their
 397 results showed that *R. macraei* is most similar to
 398 blackberry species of the subgenus *Rubus*. Moreover,
 399 they discovered that *R. macraei* and *R. hawaiiensis* are
 400 derived from separate colonizations from North America
 401 and that similarities between them are due to conver-
 402 gent evolution in the Hawaiian environment.

403 Trople and Moore (1999) calculated genetic simi-
 404 larities among 43 *Rubus* species and raspberry geno-
 405 types based on marker profiles from six RAPD
 406 primers. The similarity indices were relatively low

between the species (0.15–0.52) with much higher 407
 indices for multiple accessions within species 408
 (0.62–0.82) (Trople and Moore 1999). In another 409
 study, 40 species of *Rubus* were analyzed, including 410
 many raspberry types, using RAPD markers and 411
 showed that molecular classification of species agreed 412
 with the traditional classification of *Rubus* in most 413
 cases, except for three species in the subgenus *Mala-* 414
chobatus that clustered with the raspberry types in 415
 subgenus *Idaeobatus* (Pamfil et al. 2000). However, 416
 their RAPD-based taxonomy could not explain differ- 417
 ential success of interspecific hybridization within 418
 each subgenus. 419

9.4 Role in Development of 420 Cytogetic Stocks and Their Utility 421

A wealth of useful germplasm exists within and 422
 between the different *Rubus* species, but the complex 423
 ploidy series that exists is an obstacle to its efficient 424
 introduction into commercially important species. In 425
 order to facilitate the exploitation of existing genetic 426
 diversity, several strategies have been examined. The 427
 ploidy level of diploid *Rubus* species has been 428
 increased using colchicine on germinating seeds to 429
 generate tetraploids (Jennings and McNicol 1989; 430
 Jamieson and McLean 2008). The resulting tetraploid 431
 black and purple raspberries were reported to have 432
 larger fruit and set fruit more uniformly than diploids 433
 in cold conditions at flowering (Jennings and McNicol 434
 1989), and increased ploidy influenced flower size, 435
 flower fertility drupelet numbers, seed size, and leaf 436
 morphology (Jamieson and McLean 2008). Colchicine 437
 has also been used on tissue-cultured shoot tips to 438
 generate non-chimeral autotetraploids in *R. alleghen-* 439
niensis and *R. rusticanus* (Gupton 1989). Allopolyp- 440
 ploids were made between colchicine-doubled 441
 raspberry autotetraploids and different blackberry 442
 polyploids to make hybrid berries (Knight and Rosati 443
 1994). This material has been analyzed to confirm the 444
 nature of the hybrids using genomic and fluorescent in 445
 situ hybridization (Lim et al. 1998). A similar 446
 approach has been used with primocane fruiting, dip- 447
 loid *R. idaeus* cultivars and the resulting regenerant 448
 autotetraploids used as female parents with tetraploid 449
 and octaploid blackberries or with hexaploid hybrid 450
 berries to produce allotetraploid hybrids (Lim and 451

452 Knight 2000). Although it is technically feasible to
 453 incorporate genetic diversity between different *Rubus*
 454 species, few of the hybrids were considered to have
 455 commercial potential – most produced poor, astringent
 456 fruit, which would be commercially unacceptable
 457 (Lim and Knight 2000).

458 Blackberry breeding would also benefit from the
 459 efficient introduction of wild intra- and interspecific
 460 germplasm into breeding programs, and this would be
 461 assisted if the ploidy level of blackberries could be
 462 reduced to the diploid level (Naess et al. 1998). Ploidy
 463 reduction can happen spontaneously in plants, but it
 464 occurs rarely and methods have been developed to
 465 increase the incidence of this process, including inter-
 466 specific hybridization, interploidy crosses, improved
 467 selection techniques, chemical and physical treatments
 468 of pollen and seed parent, and in vitro culture of male
 469 and female gametophytes (reviewed by Kimber and
 470 Riley 1963; Magoon and Khanna 1963; Lacadena
 471 1974; Chu 1982; Yang and Zhou 1982). Diploid prog-
 472 eny of blackberries have been observed (Yarnell and
 473 Blackhurst 1947; Crane and Thomas 1949; Einset and
 474 Pratt 1954; Jennings et al. 1967), and more recently,
 475 strategies to produce dihaploids from tetraploid black-
 476 berry cultivars using selection of twin seed, interspe-
 477 cific hybridization, and pollen irradiation techniques
 478 have been reported (Naess et al. 1998). Of these, pollen
 479 irradiation was the most successful technique (Naess
 480 et al. 1998) and paved the way for incorporating wild
 481 *Rubus* germplasm into commercial cultivar breeding.

482 9.5 Role in Classical and Molecular 483 Genetic Studies

484 Domestication has resulted in a reduction of both
 485 morphological and genetic diversity in red raspberry
 486 (Haskell 1960; Jennings 1988) with modern cultivars
 487 being genetically similar (Dale et al. 1993; Graham
 488 and McNicol 1995). Similar work on the genetic relat-
 489 edness of black raspberries using RAPD markers was
 490 carried out and raised similar concerns with the need
 491 for greater incorporation of more diverse germplasm
 492 into black raspberry breeding (Weber 2003). Related-
 493 ness in blackberries has also been examined using
 494 pedigree analysis with similar findings recommending
 495 the diversification of the gene pool (Stafne and Clark
 496 2004). This restricted genetic diversity is of serious

concern for the future of *Rubus* breeding, especially 497
 when seeking durable host resistance to intractable 498
 pests and diseases for which the repeated use of pes- 499
 ticides in some regions is ineffective, unsustainable, or 500
 unacceptable for certain selected markets, such as 501
 “organic production.” The gene base can and is being 502
 increased by the introduction of unselected raspberry 503
 clones and species material (Knight et al. 1989). How- 504
 ever, the time required to produce finished cultivars 505
 from this material can be considerable, particularly if 506
 several generations of backcrossing are required to 507
 remove undesirable traits. 508

Breeding in *Rubus* is carried out by hybridizations 509
 between cultivars and/or species with desirable char- 510
 acteristics for multiple generations. Each cycle of 511
 crossing involves a cycle of glasshouse screening and 512
 field observation. Prior to the advent of molecular 513
 markers, inheritance and genetic mapping studies 514
 were limited to simple morphological traits (Ourecky 515
 1975; Jennings 1988). These studies generally utilized 516
 phenotypes that are deleterious in the recessive form 517
 so that they are undesirable to maintain in breeding 518
 programs. The advent of biotechnology has resulted in 519
 a fundamental shift in the development of genetic 520
 linkage maps and their use in variety development. 521
 Classical breeding, which selects parents and their 522
 desirable offspring based on an observable phenotype, 523
 is being integrated with techniques that can identify 524
 and manage genetic variability at the molecular level 525
 (protein or DNA). The ability to detect genome-wide 526
 variability has led to the characterization of genetic 527
 variation not only within coding regions (i.e., genes 528
 and their morphological manifestations) but also in 529
 non-coding regions as well, which make up large por- 530
 tions of plant genomes. These developments have 531
 enabled the construction of genetic linkage maps of 532
 red raspberry containing numerous genetic markers 533
 that are phenotypically neutral, which have been 534
 used to identify genomic regions associated with phe- 535
 notype. Corresponding mapping in blackberry and 536
 other *Rubus* species has lagged due to their complex 537
 genetic make up and/or low economic importance. 538

Early work on linkage analysis of morphological 539
 traits by Crane and Lawrence (1931) and Lewis (1939) 540
 documented aberrant segregation ratios among popu- 541
 lations segregating for fruit color (*T*) and pale green 542
 leaves (*g* or *ch*₁) in red raspberry (Crane and Lawrence 543
 1931; Lewis 1939). Further work showed genetic link- 544
 age among five genes (waxy bloom *b*, apricot or 545

546 yellow fruit *t*, pale green leaf *g*, red hypocotyl \times and
547 pollen tube inhibitor *w*), producing the first genetic
548 linkage group for *Rubus* (Lewis 1939, 1940). Sepaloid
549 *sx*₃ was later added to the linkage group between *b* and
550 *t* (Keep 1964). Crane and Lawrence (1931) and Lewis
551 (1939, 1940) also postulated on a linkage between a
552 semi-lethal allele with the unlinked *h* gene. Jennings
553 (1967) added further evidence to this linkage, propos-
554 ing the symbols *wt* for the locus linked to the fruit
555 color *t* locus and *wh* linked to the hairy locus (*h*) in
556 place of *w* that Lewis (1939) used (Jennings 1967).

557 Subsequent work in red raspberry has further elu-
558 cided the inheritance of hairiness and fruit color as
559 well as numerous other traits. Associations between
560 the *H* allele for cane hairiness and resistance to spur
561 blight, cane *Botrytis*, and cane blight have been recog-
562 nized (Knight and Keep 1958; Jennings 1988). This
563 same gene also has been associated with susceptibility
564 to cane spot, powdery mildew, and western yellow rust
565 (Jennings and McGregor 1988; Jennings and Brydon
566 1989). Similarly, the recessive gene *s* for spine-free
567 canes and the dominant *B* for waxy bloom on canes
568 can reduce spur blight incidence (Jennings 1982,
569 1988). No other linkage groups based solely on mor-
570 phological traits have been proposed. Daubeny (1996)
571 lists 72 individual loci or alleles that have been identi-
572 fied, many of which are part of an allelic series for
573 aphid resistance (Daubeny 1996). Corresponding work
574 in blackberry and other *Rubus* species has been largely
575 absent, probably due to the complex genetics of black-
576 berry and the relatively unimportant economic impact
577 of other species.

578 The first genetic map of raspberry using markers
579 was developed by Graham et al. (2004) utilizing SSR
580 and AFLPs for a population of “Latham” \times “Glen
581 Moy.” SSR markers were developed from both geno-
582 mic and cDNA libraries from the cultivar “Glen Moy.”
583 QTL analysis for variability in spine density identified
584 two associated regions on linkage group 2. Graham
585 et al. (2006) later added 20 SSR markers to the
586 “Latham” \times “Glen Moy” map along with analyzing
587 data on the *H* gene for cane hairiness and resistance to
588 multiple fungal pathogens. The *H* gene was mapped to
589 linkage group 2 and associated closely with resistance
590 to cane *Botrytis* and spur blight. Unlike previous
591 reports, no association between resistance to cane
592 spot or yellow rust and gene *H* was identified.

593 Raspberry root rot caused by *Phytophthora fragar-*
594 *iae* var. *rubi* is probably the most destructive disease in

raspberry plantations (Wilcox et al. 1993; Wilcox and 595
Latorre 2002). Resistance to *Phytophthora* root rot 596
(PRR) is found in a number of wild *Rubus* species 597
including *R. coreanus*, *R. crataegifolius* (Jennings 598
1988), and *Rubus idaeus strigosus*, the native North 599
American red raspberry, but less so in those derived 600
from *Rubus idaeus vulgatus*, the European red rasp- 601
berry (Pattison and Weber 2005). Generating crosses 602
between *R. strigosus* and *R. idaeus* can facilitate the 603
identification of the genes underpinning this resis- 604
tance. Using a “Latham” (*R. idaeus strigosus*) \times 605
“Glen Moy” (*R. idaeus vulgatus*) mapping population 606
two regions, one on each of two linkage groups have 607
been identified, and further research aimed at confirm- 608
ing these in a second population through glasshouse 609
and field trials has been completed (J. Graham, 610
K Smith and I Tierney, unpublished data). BAC clones 611
have been mapped into the resistance regions and are 612
being sequenced to identify the genes in the region 613
(J. Graham and K. Smith, unpubl data). Using an 614
RAPD-based linkage map from a cross between 615
“Latham” and “Titan,” Pattison and Weber (2005) 616
also identified markers clustered on two linkage 617
groups, which were associated with disease score 618
QTL for PRR using bulk segregant analysis. Recently, 619
this work has been extended to include AFLP, RAPD, 620
and resistance gene analog polymorphism (RGAP) 621
markers in other “Latham” and “Titan” populations 622
(Pattison et al. 2007). Considerable progress toward 623
identifying markers and ultimately the gene(s) respon- 624
sible for *R. strigosus*-based resistance to this disease is 625
being made and this can be incorporated into raspberry 626
breeding programs, allowing the rapid identification 627
and selection of durable resistant genotypes. 628

Aphids, particularly *Amphorophora idaei* (Borner) 629
and *Aphis idaei* (van der Goot), are one of the most 630
damaging arthropod pests in raspberry (Gordon et al. 631
1997) due to direct feeding damage to susceptible 632
cultivars and because they act as vectors for virus 633
transmission (McMenemy et al. 2009). Over the past 634
40 years, breeding for host plant resistance to rasp- 635
berry aphids has reduced the need for pesticides and 636
controlled the spread of aphid-borne viruses (Birch 637
et al. 2005). However, insect pests are constantly 638
adapting and overcoming plant resistance genes. Sev- 639
eral types of aphid resistance genes, minor/multi-gene, 640
and single major genes, e.g., A1 and A10, with differ- 641
ent mechanisms have been used against *A. idaei* in 642
sequence by raspberry breeders, but in the UK, each 643

644 type of major gene resistance has been broken. To
 645 date, minor gene-based aphid resistance remains dura-
 646 ble in raspberry, but it provides only partial resistance
 647 (Birch et al. 2005). Efforts to identify new sources of
 648 aphid resistance from wild species and other cultivars
 649 is underway, as is the development of molecular mar-
 650 kers to speed up the selection of promising genotypes
 651 (Birch et al. 2005). This will be facilitated by efforts to
 652 map aphid resistance genes by anchoring marker data
 653 from appropriate segregating populations to the pub-
 654 lished raspberry genetic maps (Sargent et al. 2007).
 655 Determining the map location of a number of aphid
 656 resistance genes from various sources will allow the
 657 discrimination of different genes and gene pyramiding
 658 in new raspberry cultivars.

659 Attempts to develop markers for viral resistance
 660 genes have been carried out for raspberry leaf spot
 661 and raspberry vein chlorosis utilizing the “Latham” ×
 662 “Glen Moy” cross of Graham et al. (2004). Field
 663 screening was carried out to measure symptom produc-
 664 tion of leaf spot and vein chlorosis in two different
 665 environments. These traits were analyzed for significant
 666 linkages to mapped markers, and resistance loci were
 667 found on linkage groups 2 and 8 (Rusu et al. 2006b).

668 Mapping health-related compounds is a major goal
 669 in raspberry research. The emergence of metabolom-
 670 ics makes possible the simultaneous analysis of mul-
 671 tiple metabolites at specific time points. In *Rubus*, a
 672 metabolomic approach has been used to identify bio-
 673 active compounds in a segregating mapping popula-
 674 tion planted under two different environments
 675 (Stewart et al. 2007). As a greater understanding of
 676 the relative importance and bioavailability of the dif-
 677 ferent antioxidant compounds is achieved, it may
 678 become possible to develop and identify those rasp-
 679 berry genotypes with enhanced health-promoting
 680 properties from breeding programs (Beekwilder et al.
 681 2005). Progress in mapping anthocyanins has been
 682 made by Kassim et al. (2009). Quantitative trait loci
 683 (QTL) for eight antioxidants mapped to the same
 684 chromosome region on linkage group 1 of the map of
 685 Graham et al. (2006) across both years and from fruits
 686 grown in the field and under protected cultivation.
 687 QTL for seven antioxidants also mapped to a region
 688 on LG 4 across years and for both field and
 689 protected sites. Candidate genes including a basic
 690 helix–loop–helix (bHLH) (Espley et al. 2007), a
 691 no apical meristem (NAM/CUC2_- like protein)
 692 (Ooka et al. 2003), and a basic leucine zipper (bZIP)

transcription factor (Holm et al. 2002; Mallappa et al. 693
 2006) underlying the mapped anthocyanins were iden- 694
 tified (Kassim et al. 2009). A similar approach is 695
 underway for other *Rubus* antioxidants allowing the 696
 QTL and the underlying genes to be determined, with 697
 the ultimate aim of identifying favorable *Rubus* alleles 698
 to be used in breeding programs. 699

9.6 Role in Crop Improvement Through 700 Traditional and Advanced Tools 701

Rubus breeding is hampered by several genetic pro- 702
 blems including polyploidy, apomixes, pollen incom- 703
 patibility, and poor seedling germination. The highly 704
 heterozygous nature of the germplasm requires evalua- 705
 tion of large seedling populations. Breeding is based 706
 on a generation by generation improvement in breed- 707
 ing stock through selection and intermating of indivi- 708
 duals showing promise of producing superior progeny. 709
 This average improvement in the progeny of breeding 710
 stock resulting from intermating selected parents is 711
 called response to selection (see review Hansche 712
 1983). Several excellent reviews of blackberry and 713
 raspberry breeding have been written in the past few 714
 years including Finn and Knight (2002a, b), Clark 715
 et al. (2007), Finn (2008), Finn and Hancock (2008). 716

717 The incorporation of novel resistance/tolerance to
 718 pests and diseases is regarded as essential for the
 719 development of cultivars suitable for culture under
 720 integrated pest management (IPM) systems. Sources
 721 of resistance in diverse *Rubus* spp. to many pests and
 722 diseases have been identified and exploited in conven-
 723 tional cross-breeding (Keep et al. 1977; Jones et al.
 724 1984; Jennings 1988; Knight 1991; Williamson and
 725 Jennings 1992). However, germplasm bearing single
 726 resistance genes, when planted over extensive areas,
 727 can eventually be overcome by the rapid evolution of
 728 new biotypes of pests, so that new types of host resis-
 729 tance are required to sustain plant protection (Birch
 730 et al. 2002; Jones et al. 2002). Pest and diseases of
 731 raspberry in Europe have been extensively reviewed in
 732 Gordon et al. (2006).

733 Pattison et al. (2007) combined generational means
 734 analysis with molecular markers and QTL analysis to
 735 map resistance to *Phytophthora* root rot in a BC₁ popu-
 736 lation of NY00-34 (“Titan” × “Latham”) × “Titan.”

737 Separate genetic linkage maps of NY00-34 and “Titan”
738 were developed using RAPD, AFLP, and RGAP and
739 analyzed for QTL associated with various parameters
740 of root rot resistance assayed in a hydroponic system
741 (Pattison et al. 2004).

742 *Agrobacterium*-mediated genetic transformation
743 techniques for *Rubus* have been described in the liter-
744 ature (Graham et al. 1995; Mathews et al. 1995;
745 Kokko and Kärenlampi 1998), and transgenic rasp-
746 berry plants have been generated that are resistant to
747 raspberry bushy dwarf virus (Malowicki et al. 2008)
748 and that contain a modified auxin synthesizing gene to
749 enhance fruit productivity (Mezzetti et al. 2004).
750 Should potentially favorable alleles conferring desir-
751 able characters be identified in wild *Rubus* species, it
752 may be technically feasible for these to be
753 incorporated into existing commercial cultivars.
754 Whether genetic modification is a commercially
755 acceptable way to producing improved *Rubus* culti-
756 vars remains to be seen.

757 9.7 Genomics Resources Developed

758 The advances in genomics technologies have led to a
759 massive increase in the numbers of DNA sequences
760 held in public databases, and the numbers of *Rubus*
761 sequences are very likely to increase rapidly as efforts
762 are under way to sequence EST libraries generated
763 from different tissues and developmental stages. At
764 SCRI, cDNA libraries have been generated from
765 leaves (approximately 6,500 clones), canes (approx-
766 imately 8,000 clones), and roots (approximately 7,300
767 clones), and new generation sequencing has been used
768 to identify gene transcripts in ripening fruit (J. Graham,
769 K. Smith, M. Woodhead, and S. McCallum, unpubl
770 data). Besides providing sequence information on
771 genes expressed in these tissues, these resources are
772 being used to identify gene-based markers for use in
773 the genetic mapping programs. A project to character-
774 ize bud dormancy phase transition in woody perennial
775 plants at a molecular level generated a total of 5,300
776 ESTs from endodormant (true dormancy) and para-
777 dormant (apical dominance) raspberry meristematic
778 bud tissue (Mazzitelli et al. 2007). PCR products
779 from these cloned cDNA fragments have been spotted
780 onto glass slides and have been used in microarray
781 experiments to identify genes that show differential

expression. At present, approximately 380 782
clones exhibit up- or downregulation during the endo- 783
dormancy–paradormancy transition. Some of these 784
ESTs, including one encoding a MADS-box gene, a 785
MYB gene, and several containing SSRs, have been 786
identified and mapped in the “Latham” × “Glen Moy” 787
mapping population, and these underlie ripening QTL 788
(Graham et al. 2009b). 789

Genes upregulated during fruit ripening have been 790
identified using classical plus/minus screening of 791
cDNA libraries (Jones et al. 1998) and RNA finger- 792
printing techniques (Jones et al. 2000). Among the 793
genes identified were cell wall hydrolases involved 794
in fruit softening and ACC oxidase (Jones et al. 795
2000) involved in the ethylene biosynthetic pathway. 796

The phenylpropanoid pathway is important in rasp- 797
berry as end products contribute to the color and 798
aroma of the fruit and are involved in other processes 799
such as lignin production. Aroma and color in rasp- 800
berry fruit are partly derived from the polyketide deri- 801
vatives benzalacetone and dihydrochalcone, which are 802
formed during fruit ripening as a result of the action of 803
several enzymes, polyketide synthases (PKS), benza- 804
lacetone synthase, and chalcone synthase (CHS) dur- 805
ing fruit development. A number of PKS genes have 806
been characterized from raspberry (Zheng et al. 2001; 807
Kumar and Ellis 2003a). Kumar and Ellis (2003a) 808
reported that the PKS gene family in *Rubus* consists 809
of at least 11 members, and the expression analysis of 810
three cDNAs showed that they exhibited tissue-specific 811
and developmental patterns of expression, with two 812
cDNAs upregulated during fruit ripening. More 813
recently, the cloning of a raspberry benzalacetone 814
synthase (PKS4) has been reported (Zheng and 815
Hrazdina 2008). 816

Genes encoding 4-coumarate: CoA ligase, an 817
enzyme that activates cinnamic acid and its derivatives 818
to thioesters, which then serve as intermediates for the 819
production of phenylpropanoid-derived compounds 820
that influence fruit quality have also been studied. 821
Kumar and Ellis (2003b) have characterized the 822
4-coumarate: CoA ligase (4CL) genes in raspberry 823
found there are three genes, which are differentially 824
expressed in various organs and during fruit develop- 825
ment and ripening. Based on the expression patterns 826
and substrate utilization profiles of the recombinant 827
proteins, they suggest that 4CL1 is involved in the 828
biosynthesis of phenolics in leaves, 4CL2 in cane 829
lignification and 4CL3 in the flavonoid and/or flavor 830

831 pathway in fruit. These genes are also being targeted
832 in the *Rubus* mapping program (M. Woodhead,
833 J. Graham and K. Smith personal communication).

834 The first publicly available red raspberry BAC
835 library from the European red raspberry, "Glen
836 Moy," has been constructed comprising over 15,000
837 clones with an average insert size of approximately
838 130 kb (6–7 genome equivalents). Hybridization
839 screening of the BAC library with chloroplast (*rbcL*)
840 and mitochondrial (*nad1*) coded genes revealed that
841 contamination of the genomic library with chloroplast
842 and mitochondrial clones was very low (>1%) (Hein
843 et al. 2005). Initial screening of the BAC library
844 employed probes for chalcone synthase, phenylalanine
845 ammonia lyase, and a MADS-box gene involved in
846 bud dormancy (I. Hein and S. Williamson personal
847 communication). More recently, the library has been
848 probed with genes involved in fruit quality genes
849 (M. Woodhead and S. McCallum personal communi-
850 cation) and a peach ever-growing gene (A. G. Abbott
851 personal communication) and with markers underly-
852 ing QTL for Phytophthora root rot resistance.

853 9.8 Scope for Domestication and 854 Commercialization

855 Berries are extremely high in antioxidants, exhibiting
856 up to four times more antioxidant capacity than non-
857 berry fruits, 10 times more than vegetables and
858 40 times more than cereals (Halvorsen et al. 2002).
859 They contain high levels of the antioxidant vitamins
860 A, C, and E and very high levels of non-essential but
861 strongly antioxidant phenolic compounds. Phenolics
862 can account for 90% or more of the overall antioxidant
863 capacity found in berry fruit (Deighton et al. 2000), the
864 most readily visible of which are the anthocyanin
865 pigments. These pigments impart the deep, vibrant
866 colors of berries and can be found at concentrations
867 of up to 500 mg 100 g FW⁻¹. Berries represent a
868 significant dietary source of anthocyanins, as only 24
869 out of 100 common foods contain anthocyanins, and
870 non-berry anthocyanin-containing foods typically
871 contain less than 100 mg 100 g FW⁻¹ (Wu et al.
872 2006).

873 The shift in focus from vitamin C and micronutrients
874 toward the polyphenolics causes something of a chal-
875 lenge for any breeding effort, since the polyphenolics

are chemically diverse and the content of individual
876 health-promoting compounds varies in raspberry
877 fruit due to both developmental and genetic factors
878 (Beekwilder et al. 2005). However, with the emer-
879 gence of metabolomics, the simultaneous analysis of
880 multiple metabolites at specific time points is now
881 feasible. In *Rubus*, a metabolomic approach has been
882 used to identify bioactive compounds in a segregating
883 mapping population planted under two different envir-
884 onments (Stewart et al. 2007). As a greater understand-
885 ing of the relative importance and bioavailability of
886 the different antioxidant compounds is achieved, it
887 may become possible to develop and identify those
888 raspberry genotypes with enhanced health-promoting
889 properties from breeding programs (Beekwilder et al.
890 2005) and to mine for favorable alleles from
891 wild *Rubus* accessions for inclusion into breeding
892 programs.
893

The traditional medicinal uses of different *Rubus*
894 species are well known and have recently been
895 reviewed (Patel et al. 2004). *R. idaeus* leaves and
896 roots are anti-inflammatory, astringent, decongestant,
897 ophthalmic, oxytocic, and stimulant (Grieve 1971;
898 Triska 1975; Foster and Duke 1990; Chevallier
899 1996). A tea made from them is used to treat diarrhea
900 and as a tonic for pregnant women (only in the last
901 3 months of pregnancy) to strengthen the uterus in
902 preparation for childbirth (Foster and Duke 1990).
903 Externally, the leaves and roots can be used to treat
904 tonsillitis, mouth inflammations, and as a poultice to
905 treat sores, conjunctivitis, minor wounds, and burns
906 (Bown 1995; Moerman 1998). The Kiowa and Apache
907 made a tea from the roots of *R. occidentalis* species to
908 treat stomach ache and blackberry root tea was part of
909 the treatment for hemorrhaging and hemophilia
910 (<http://www.biosurvey.ou.edu/shrub/rubu-occ.htm>).
911 *Rubus fruticosus* roots infused in water with penny-
912 royal (*Mentha pulegium*) were used in the treatment of
913 bronchitis and asthma and the leaves used as an astrin-
914 gent against bacterial infections (Beith 1995). Rasp-
915 berry leaf tea is probably the most widely known
916 herbal product associated with *Rubus*, but the value
917 of natural components within *Rubus* are still being
918 realized.
919

Fruits from *Rubus* are antiscorbutic (i.e., prevent
920 scurvy) and diuretic (Chiej 1984), and recent evidence
921 suggests that fruit polyphenol components may affect
922 activities of digestive tract enzymes and may provide a
923 means for controlling diseases such as type 2 diabetes
924

925 (McDougall and Stewart 2005). The antioxidant com- 974
 926 pounds present in black raspberry berries are being 975
 927 evaluated for the topical treatment of human pre- 976
 928 malignant oral lesions (Mallery et al. 2007, 2008), 977
 929 and freeze dried black raspberries and raspberry 978
 930 extracts are being assessed for the prevention of 979
 931 esophageal and colon cancer (Stoner et al. 2007). 980
 932 Raspberry fruits contain complex phenolic com- 981
 933 pounds, e.g., ellagitannins, which are strong anti-
 934 microbial agents against, for example, *Salmonella* and
 935 *Staphylococcus* (Puupponen-Pimiä et al. 2005) and
 936 may have applications in both medicine and the food
 937 industry in the future.

938 It has been reported that topical application of
 939 raspberry ketone (4-(4-hydroxyphenyl)butan-2-one),
 940 the compound that gives raspberry fruit their charac-
 941 teristic aroma, can promote hair re-growth in some
 942 humans with alopecia and increase skin elasticity
 943 (Harada et al. 2008) and, in mice, prevents and
 944 improves obesity (Morimoto et al. 2005).

945 Patel et al. (2004) recently reviewed the volatile
 946 components occurring in a number of *Rubus* species.
 947 Not only do different *Rubus* species produce different
 948 types of volatile, the relative proportions of the vola-
 949 tiles produced can change during plant growth in
 950 raspberry and those emitted during flowering act as
 951 attractants to pollinating insects (Robertson et al.
 952 1995). The total amount and type of volatiles pro-
 953 duced from ripe blackberry fruit varies significantly
 954 between cultivar (Qian and Wang 2005) and in rasp-
 955 berry, although ethyl acetate at 12–18% was found
 956 to be the major detectable volatile product of ripe
 957 raspberry fruit (Robertson et al. 1995), it is not the
 958 major aroma compound. This is attributed to rasp-
 959 berry ketone, a compound widely used in perfumery,
 960 in cosmetics, and as a food additive to impart a fruity
 961 odor. This natural compound (also known as 4-(4-
 962 hydroxyphenyl)butan-2-one) is a derivative of the
 963 phenolic pathway, and although it is the primary
 964 aroma compound of red raspberries (Hradzina 2006),
 965 it is found in low quantities in plants, between 1 and
 966 17 µg/100 g FW (Borejsza-Wysocki et al. 1992).
 967 Demand for raspberry ketone is growing consider-
 968 ably, and although it can be produced by organic
 969 synthesis, work is underway to better understand
 970 how this compound is produced in planta. A raspberry
 971 gene encoding a benzalacetone synthase (or polyke-
 972 tide synthase 4, PKS4) has recently been reported
 973 (Zheng and Hrazdina 2008) and paves the way for

producing this flavor compound using alternative stra- 974
 tegies such as microbial fermentation. Due to the 975
 sensory importance of this compound in fresh and 976
 processed raspberry products (Larsen et al. 1991), it 977
 would be desirable to screen raspberry germplasm for 978
 genotypes containing naturally high levels of rasp- 979
 berry ketone to improve the sensory characteristics 980
 of fruit through breeding. 981

9.9 Some Dark Sides and Their Addressing 982

Rubus species are typically found as early colonizers 984
 of disturbed sites such as pastures, along forest edges, 985
 in forest clearings, and along roadsides. Blackberries 986
 are typically much more tolerant of drought, flooding, 987
 and high temperatures, while red raspberries are more 988
 tolerant of cold winters. Most species are polyploid, 989
 facultatively apomictic, and pseudogamous (i.e., pol- 990
 lination is required to trigger endosperm development 991
 in the seed (Gustafsson 1943)). Additionally, they 992
 exhibit vigorous vegetative reproduction by either tip 993
 layering or root suckering, permitting *Rubus* geno- 994
 types to cover large areas (Werlemark and Nybom 995
 2003). The attractiveness of the fruits to frugivores, 996
 especially birds, means that seed dispersal can be 997
 widespread with the result that *Rubus* genotypes can 998
 very easily be spread to new sites. The overall effect – 999
Rubus spp. are very effective, high-speed invaders 1000
 (Greimler et al. 2002; Baret et al. 2004). 1001

1002 Like many plant species that have since become 1002
 invasive weeds, *Rubus* spp. typically moved around 1003
 the world by humans who introduced them as food 1004
 crops or as a result of trading activities (Ellison and 1005
 Barreto 2004). Certain *Rubus* species have become 1006
 very problematic in some regions of the world (Daehler 1007
 1998) where they produce very dense, impenetrable 1008
 thickets, which make it impossible for native flora to 1009
 germinate and establish, and they can also form 1010
 hybrids with native species. As well as contributing 1011
 to the obvious loss in biodiversity, these weeds pose a 1012
 serious financial problem to agriculture, and efforts to 1013
 find effective solutions to control them continue. 1014

1015 There are many alien *Rubus* species and here we 1015
 present several examples and the problems they 1016
 pose and, in some cases, the strategies employed to 1017
 control them. 1018

1019 Blackberry (*R. fruticosus* L. aggregate) is an impor- 1068
1020 tant weed in both agricultural and natural ecosystems in 1069
1021 Australia, covering some 8.8 million ha. It is regarded 1070
1022 as one of the worst weeds in Australia because of 1071
1023 its invasiveness, potential for spread, and economic 1072
1024 and environmental impacts ([http://www.weeds.gov.au/](http://www.weeds.gov.au/publications/guidelines/wons/pubs/r-fruticosus.pdf) 1073
1025 [publications/guidelines/wons/pubs/r-fruticosus.pdf](http://www.weeds.gov.au/publications/guidelines/wons/pubs/r-fruticosus.pdf)).

1026 At least 15 different but closely related species of 1074
1027 blackberry are naturalized in Australia (Evans et al. 1075
1028 2005). Accurate taxonomic keys are important to 1076
1029 determine which taxa are contributing to the problem, 1077
1030 and DNA fingerprinting is important as a tool in this 1078
1031 area (Evans et al. 1998, 2007). This is particularly 1079
1032 relevant for applying biological control measures 1080
1033 because blackberry leaf rust (*Phragmidium viola-* 1081
1034 *ceum*) is ineffective against some European blackberry 1082
1035 species and all American blackberry species (Scott 1083
1036 et al. 2008). An additional biological control agent, 1084
1037 the redberry mite, *Acalitus essigi* (Hassan), is under 1085
1038 evaluation to aid control of blackberry (Scott et al. 1086
1039 2008), but other measures such as herbicides, mechan- 1087
1040 ical removal, and burning are still required to control 1088
1041 this weed. 1089

1042 In Chile, two weedy species of blackberry, *R. con-* 1090
1043 *strictus* Lef. & M. (native to central Europe) and 1091
1044 *R. ulmifolius* Schott (native to the Mediterranean), 1092
1045 both introduced in the second half of the nineteenth 1093
1046 century, have become naturalized and were estimated 1094
1047 to cover 5 million ha by 1973 (Ellison and Barreto 1095
1048 2004). As in Australia, the use of *P. violaceum* has 1096
1049 proved effective in controlling these species, particu- 1097
1050 larly *R. constrictus*, the more problematic of the two 1098
1051 weeds, without affecting the commercial species 1099
1052 *R. idaeus* L. and *R. loganobaccus* (loganberry). The 1100
1053 rust hastens normal defoliation, and infected stems do 1101
1054 not lignify properly, which increases susceptibility to 1102
1055 infection by other pathogens and to frost damage 1103
1056 (Oehrens and Gonzalez 1977). Such weakened plants 1104
1057 are less competitive and are displaced by native spe- 1105
1058 cies (Oehrens 1977). 1106

1059 In Hawaii, there are two endemic *Rubus* species: 1107
1060 *R. hawaiiensis* A. Gray, a major component of the 1108
1061 forest ecosystem above 200 m elevation, and 1109
1062 *R. macraei* A. Gray, which is less widely distributed. 1110
1063 Both have North American ancestry (Howarth et al. 1111
1064 1997; Morden et al. 2003) and are partly sympatric 1112
1065 with seven alien *Rubus* species that are naturalized in 1113
1066 the Hawaiian islands (Randell et al. 2004) including 1114
1067 *Rubus rosifolius*, a native to Australia. Apart from the 1115

1068 threat of these *Rubus* species to invade and dominate 1069
1070 existing forest, hybrids between *R. rosifolius* and 1071
1072 *R. hawaiiensis* have been found (Randell et al. 2004). 1073
1074 Studies have shown the hybrids to be sterile, so 1074
1075 although this may preclude genetic assimilation of 1075
1076 *R. hawaiiensis* by *R. rosifolius* and the acquisition 1076
1077 of favorable, adaptive alleles by *R. rosifolius* from 1077
1078 *R. hawaiiensis*, nevertheless, the production of non- 1078
1079 viable seed by *R. hawaiiensis* represents a loss of 1079
1080 reproductive effort and may have a negative impact 1080
1081 on the species, and the hybrids may well have an 1081
1082 advantage and pose a competitive threat (Randell 1082
1083 et al. 2004). 1083

1084 *Rubus armenicus* is now a serious invasive weed in 1084
1085 the USA and Australia. Native to Armenia in South- 1085
1086 west Asia, it was introduced to Europe in 1835 and 1086
1087 Australasia and North America in 1885. It was valued 1087
1088 for its large, sweet fruit, similar to that of common 1088
1089 blackberries (*R. fruticosus*) and attractive for domestic 1089
1090 and commercial fruit production (cultivars “Himala- 1090
1091 yan Giant” and “Theodore Reimers” are particularly 1091
1092 commonly planted (Ceska 1999)). 1092

1093 *R. alceifolius* Poir., a bramble, is native to south- 1093
1094 eastern Asia and Malaysia and has been introduced to 1094
1095 the Indian islands of Madagascar, Mayotte, La 1095
1096 Reunion, and Mauritius where it is a serious weed, 1096
1097 and to Queensland, Australia (Amsellam et al. 2001a, 1097
1098 b). Reductions in the level of genetic diversity of the 1098
1099 populations in areas of introduction were found and 1099
1100 within the Indian islands, each population examined 1100
1101 was characterized by a single clone, which was closely 1101
1102 related to individuals from Madagascar (Amsellam 1102
1103 et al. 2000). Amsellam et al. (2001a, b) suggest that 1103
1104 there is a switch in the reproductive biology in this 1104
1105 species. In its native range, *R. alceifolius* produces seed 1105
1106 sexually, the plants in Madagascan populations are 1106
1107 hybrids between *R. alceifolius* and native populations 1107
1108 of *R. roridus* and produce seed mostly apomictically, 1108
1109 while plants from Reunion Island (where *R. alceifolius* 1109
1110 was introduced in 1850) produce seed exclusively 1110
1111 apomictically. Considerable variation in fertility and 1111
1112 vegetative growth in this species on Reunion Island 1112
1113 has been described; fruit set is decreased in plants at 1113
1114 increasing elevations, but this may be compensated for 1114
1115 by greater vegetative growth (Baret et al. 2004). 1115

1116 Gene flow between distantly related *Rubus* species 1116
1117 has been demonstrated by the presence of naturally 1117
1118 occurring hybrids between *R. caesius* (a facultatively 1118
1119 agamous tetraploid blackberry) and diploid *R. idaeus* 1119
1120 1120

1117 in Europe (Alice et al. 2001), and the presence of
 1118 hybrids between *R. alceifolius* and *R. roridus* in Mada-
 1119 gascar (Amsellam et al. 2001a, b). Luby and McNicol
 1120 (1994) surveyed wild and feral *Rubus* populations in
 1121 Scotland for evidence of the escape of two genes, L_1
 1122 (for fruit size and plant morphology) and s (for spine-
 1123 lessness), introduced into raspberry cultivars by tradi-
 1124 tional breeding in the previous 20–30 years. The L_1
 1125 gene was not found and very low frequencies of the
 1126 s gene (0.004) were found in wild *R. ideaus* popula-
 1127 tions within the locale of the commercial planting area
 1128 but not in populations remote from commercial pro-
 1129 duction. Thus, should transgenic *Rubus* crops be
 1130 deployed, there is potential for escape into sympatric
 1131 wild populations, although this was considered to
 1132 probably be infrequent (Luby and McNicol 1994).
 1133 More recently, Graham et al. (2009a) demonstrated
 1134 that limited gene flow into a wild *R. ideaus* population
 1135 occurred but that pollen movement was hindered
 1136 between populations at different altitudes, probably
 1137 because of differences in flowering time. This gene
 1138 flow into one population was identified by the gain of
 1139 one new allele into progeny at the site; however, work
 1140 also showed that three alleles were lost from parents to
 1141 progeny, highlighting the flux in genetic diversity in
 1142 natural populations.

1143 9.10 Recommendations for Future 1144 Actions

1145 With the narrowing genetic base of our cultivated
 1146 fruits, coupled with the increasing demands from con-
 1147 sumers, new breeding methods are required to meet
 1148 demands. Concern over the environmental impact and
 1149 sustainability of agricultural and horticultural prac-
 1150 tices is leading to a greater emphasis on pest and
 1151 disease resistance, as well as the ability of plants to
 1152 withstand local environmental stresses. The changes
 1153 in environmental, cultural, and agronomic practices
 1154 within the industry will impact strongly on the nature
 1155 of the germplasm required for the future. Greater con-
 1156 servation of genetic resources and utilization of
 1157 diverse, locally adapted germplasm will be required
 1158 for the future viability of *Rubus* production. Neverthe-
 1159 less, the development of molecular and genetic tools
 1160 to link genotype to phenotype in *Rubus* mapping popu-
 1161 lations segregating for key characteristics and the

1162 identification of favorable alleles from diverse germ- 1162
 1163 plasm may allow for more rapid and targeted deploy- 1163
 1164 ment of genes controlling these important traits, 1164
 1165 whether by marker assisted breeding (MAB) or 1165
 1166 through other means such as genetic modification 1166
 1167 (GM). 1167

1168 The changing climate is already a major consider- 1168
 1169 ation for soft fruit growing due to the succession of 1169
 1170 mild winters, leading to poor bud break in some fruit 1170
 1171 species, and this may be addressed by employing a 1171
 1172 locally adapted germplasm. 1172

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