Julie Graham · Rex Brennan *Editors*

Raspberry

Breeding, Challenges and Advances

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Preface

This book is intended as an update to *Raspberries and Blackberries: Their Breeding, Diseases and Growth* by D.L. Jennings, published in 1988 by Academic Press. All of the content of Jennings, 1988 is still relevant today; however, there have been significant advances and challenges in a number of areas including variety development and molecular breeding technologies, the impacts of climate change, lack of active compounds allowed for use on crops, the use of agroecology principles in plant defense, and new high-throughput plant phenotyping method developments. This book, which is focused on raspberry alone, aims to capture some of these advances as a companion to the 1988 text.

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Chapter 1
Introduction to the *Rubus* Genus

Julie Graham and Rex Brennan

1.1 Taxonomy, Botany and Growth

Raspberries, blackberries and the associated hybrid berries belong to the genus *Rubus* in the Rosaceae. The genus comprises of a highly diverse series of over 700 species with a chromosome number of x = 7 and ploidy levels ranging from diploid to dodecaploid (Jennings 1988; Meng and Finn 2002). The centre of diversity for *Rubus* is thought to be in China (Thompson 1997). Members of the genus can be difficult to classify into distinct species due to hybridization and apomixis, but molecular studies (Alice and Campbell 1999; Sochor et al. 2015; Wang et al. 2016) are now assisting the development of a robust phylogeny for *Rubus.* A brief history of the crop from ancient times can be found in Roach (1985) and Swanson et al. (2011) and Chap. 2 of this volume. However, the development of blackberry and raspberry as crops is much more recent, with cultivated forms of raspberry appearing in Europe in the mid-sixteenth century, although distinct cultivars were not reported until the late eighteenth century (Jennings 1995). Controlled breeding of raspberry began in the 1920s, and increased to the point where over 100 cultivars were released between 1981 and 2001 (Moore 2008). In the case of blackberry, cultivated forms appeared around 1830, and the development of the 'Loganberry' in 1890 is considered to be the first breeding effort in this crop (Swanson et al. 2011). The most widely grown blackberry cultivar is 'Marion', a trailing type, which is grown on over 2500 ha in Oregon alone (Finn 2008).

A comprehensive list of *Rubus* species, subgenera and sections is provided by Skirvin et al. (2005). The commercially important domesticated berries are contained within two subgenera, Idaeobatus and Eubatus. Idaeobatus contains the European red raspberry R. *idaeus* L. subsp. *idaeus,* the North American red raspberry *R. idaeus* subsp. *strigosus* Michx. and the black raspberry *R. occidentalis* L. Species

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within the Idaeobatus are distributed mainly in northern Asia but also East and South Africa, Europe, Australia and North America (Jennings 1988). Members of the Idaeobatus subgenus are distinguished by the ability of their mature fruits to separate from the receptacle. Almost all of the raspberry species are diploid (Thompson 1995), with only occasional variations as triploids or tetraploids.

In contrast, the Eubatus subgenus containing the blackberries (*R. fructicosus* and *R. caesius,* plus the North American *R. ursinus*) has a considerably more complex genetic makeup, and is mainly distributed in South America, Europe and North America (Jennings 1988). In terms of climate resilience, blackberries are more tolerant of drought, flooding and high temperatures than most raspberries, while the latter are more tolerant of cold winters. Plants exhibit vigorous vegetative reproduction by either tip layering or root suckering, permitting *Rubus* to cover large areas in some cases.

Raspberries and blackberries are woody perennial plants with a biennial cane habit, though primocane varieties (also referred to as fall-bearing) that fruit annually are increasingly important commercially, mainly because they provide an opportunity to extend the cropping season into late summer and beyond. Additionally, especially in regions with low chilling, primocane raspberry cultivars can be managed to produce a double crop in both summer and autumn (Pritts 2008).

Both types of raspberry form new shoots in the spring, followed by vegetative growth throughout the summer. In primocane varieties, flowers are initiated in mid-summer and develop to produce fruit in the autumn. In biennial fruiting varieties, floral initiation does not occur until the autumn, with fruiting occurring in the second year of development.

Changes in day length and temperature cause shoot elongation to cease, and the leaves form a terminal rosette at the shoot tip, after which dormancy sets in gradually. The environmental control of growth and flowering/fruiting in raspberry is reviewed by Moore and Caldwell (1985), Carew et al. (2001), Heide and Sønsteby (2011) and Graham and Simpson (2018).

Most blackberries and black or purple raspberries continue growth into the autumn and do not form a rosette, with growth stopped by rooting at the tips in contact with the ground or low temperatures. Age, genotype and environmental conditions play a role in timing and intensity of dormancy. Additionally, there appears to be some variation in the depth of dormancy achieved by some raspberry cultivars (Heide and Sønsteby 2011; N. Jennings pers. comm.).

The flowers have five sepals, five petals, a very short hypanthium, many stamens, and an apocarpous gynoecium of many carpels on a cone-like receptacle. Multiple ovaries each develop into a drupelet and the aggregate fruits are composed of the individual drupelets held together by almost invisible hairs.

Strik (1992) classified commercial blackberries into three groups based on plant habit, specifically trailing, semi-erect and erect. The trailing types such as ‘Marion’ form crowns with the primocanes trailing on the ground, where they are gathered and tied to a trellis. The semi-erect types grow on a trellis before arching over, and include ‘Loch Ness’ and ‘Chester’, while the erect types, such as ‘Navaho’ and

'Natchez', grow upright and do not form crowns directly, producing suckers below the soil instead.

In favourable conditions plantations can continue to fruit for more than 15 years and in some isolated parts of central Europe there are plantations aged 25 years or more. However, pest and disease pressures, together with changes in production methods, have ensured that plantation life can be seriously curtailed to uneconomic levels if the problems are not adequately addressed.

1.2 Economic Importance

Fruit of *Rubus* species represent a valuable horticultural commodity, providing both a source of income and also labour, as most fruit for the high-value fresh market is hand-harvested. After fresh fruit, individually quick frozen (IQF) berries are the next most valuable, and can either be hand- or machine-harvested (Moore 2008). The crops are also produced for processing markets, including high value berry juices for their flavour and perceived health benefits, and machine harvesting is usually normal for these markets.

Demand for raspberries, blackberries and other *Rubus* spp. is increasing rapidly in Europe and elsewhere (Clark et al. 2007; Strik et al. 2007, Swanson et al. 2011; Finn and Strik 2016), mainly due to improved shelf-life and fruit quality for the consumer through the use of refrigerated transport and storage, but also in part due to perceived health benefits. Across large parts of Europe especially, production of *Rubus* fruits for the fresh market is now largely conducted under polytunnels of varying design (Figs. 1.1 and 1.2), to give optimal growing conditions and the ability to extend the cropping season beyond the traditional short summer period. To meet the rising demand for berries on a year-round basis and to address the emerging

Fig. 1.1 High density production of *Rubus* under polytunnels

Fig. 1.2 New release Glen Carron from the commercially funded James Hutton Limited raspberry programme

challenges of environmental impacts and climate change, new cultivars are urgently required from plant breeders. In order to achieve this goal, breeders require several key resources; some are self-evident, eg. appropriate germplasm to enable the introgression of important traits into new cultivars, but contemporary breeding can also now utilise 'omics' technologies and phenotyping platforms to develop suitable cultivars in a more targeted manner than previously possible.

Rubus crops are of global significance in their production and value. For red raspberry, the biggest production is in Europe where the largest output is from Serbia, Russia and Poland, followed by the UK, Spain and Portugal, particularly for the fresh market. Figure 1.1 shows high density plantings under tunnel. Out-with Europe, the biggest producers of raspberry are the USA and Chile. Black raspberries are predominantly grown in North America for both the fresh and processing markets, with Oregon the leading production area, although there is also significant production in the eastern USA, and also in Korea. In recent years the demand for blackberries has increased sharply, particularly in Europe which now has the largest acreage in production. In North America, the main production of blackberries is also located in Oregon, and US production in 2014 was valued at over $50 m (National Agricultural Statistics Service, USDA, 2015). Mexican production of blackberry has increased significantly in recent years, mainly due to the opportunities for export and season extension to the USA, and raspberry is also exported in this way. Blackberries are also produced in Central America (Costa Rica and Guatemala) and in South America (predominantly from Ecuador and Chile). In Asia, China has seen a rapid expansion in production across several provinces. Production in

Oceania is mainly in New Zealand, particularly of the Boysenberry, and temperate parts of Australia, although the areas planted are relatively small. African production is in South Africa, Morocco, Algeria and Kenya.

There is localized interest in other *Rubus* species, notably in sub-arctic areas. Cloudberry (*Rubus chamaemorus*), in the subgenus Chamaemorus, is a highly valued berry in Scandinavia and northern Russia, with potential for domestication (Korpelainen et al. 1999). Similarly, the arctic bramble *Rubus arcticus* is grown for both fresh and processing purposes in Finland and northern latitudes in Scandinavia and North America (Ryynänen 1972), although production is often curtailed by various disease problems (Kokko et al. 1999; Lindqvist-Kreuze et al. 2003).

1.3 Climate Effects and Stress Tolerance

Abiotic and biotic stresses, both current and emerging, can limit crop productivity so resistant and resilient germplasm is required for cultivar development. Water stress is also forecast to increase at certain times of the year, with more erratic annual rainfall distribution described in many future climate models (IPCC 2014), intensified by soil physical conditions imposed by cultivation. Additionally, the cost of irrigation is likely to increase, so the selection of drought tolerant (DT) and water use efficient (WUE) genotypes will be crucial for some areas. For example, in the UK access to groundwater is now controlled through a government licensing programme, and abstraction licences are granted on the basis of availablity of water with no guarantee that applicants will be granted access to the volumes of water required to grow crops. In England, >50% of soft fruit holdings are in catchments defined as having no water available or defined as over-abstracted (HDC Project Report CP64, 2009). Conversely, cultivars tolerant to wetter flooded conditions may be required in other areas where climate change predictions suggest significant increases in rainfall.

Most *Rubus* plants require some level of chilling to develop normally from bud-break in the following season, and there is some variation between cultivars in this chill requirement. As the climatic trend is towards warmer winters, with less chilling hours, this may become an issue for plant breeders and the future sustainability of *Rubus* crops, particularly red raspberry. Most *Rubus* cultivars will not withstand winter temperatures below around – 30 °C (Moore 2008), although blackberries are more vulnerable to winter injury than raspberries. For a review of heat stress see Fernandez et al., Chap. 3.

High throughput phenotyping methods with the potential to accelerate both the assessment of crop performance under differing regimes and the identification of useful phenotypes for future production are under development, and several phenotyping platforms currently exist (eg. www.plant-phenomics.ac.uk/en/resources/lemnatec-system; http://www.plantphenomics.org.au/). However, these currently operate under artificially controlled conditions, and development of in-field phenotyping platforms is underway in berry crops including raspberry, which will enable improved selection regimes for research and plant breeding (see

Chap. 9, Williams et al.). In addition to advances in phenotyping, significant advances in genomics and metabolomics technologies are increasing our understanding of the links between genotype, phenotype and environment, with molecular tools emerging to assist and inform varietal selection strategies (see Chap. 8, McCallum et al.).

1.4 Cultivation and Challenges

The lifespan of most *Rubus* plantations is limited by a number of constraints predominantly linked to pest and pathogen pressures (see Chaps. 4 and 5) and crop biology (see Chap. 2). The plant's physical or architectural characteristics may therefore play a role in the viability of plantations. Plants with certain physical characteristics may be able to resist pests and diseases by exploiting morphological structures or biomechanical characteristics that interfere with pest/pathogen movement, host recognition, feeding or reproduction on or in the plant (Hanley et al. 2007), by making the plant less attractive visually, or presenting physical barriers to pests and diseases (Mitchell et al. 2013). Architectural traits in raspberry such as bush density and leaf hairs were shown to increase pest burden (Graham et al. 2014). Some plant traits however offered benefits, eg. cane hairs protect against fungal diseases (Graham et al. 2009a). Recently, Mitchell et al. (2016) reviewed the current understanding of the utility of herbivore resistance and tolerance traits as a strategy for improving the sustainability of crop protection, and the use of agro-ecological principles in resistance traits is discussed further in Chap. 5.

The planting of fully disease-free certified *Rubus* stocks into clean soils free from persistent viral, bacterial and fungal diseases and certain pests has a major bearing on the lifespan of plantations. These issues are underpinned by effective and robust quarantine arrangements and certification schemes to protect the propagation industry and downstream fruit production (Jones 1991; Smith 2003). Further information on plant certification highlighting the UK system as a case study is given in Chap. 6 of this volume.

Other crop management issues for *Rubus* fruits includes control of root spread across the inter-row space, requiring these young canes ('suckers' or 'spawn') be removed, mechanically or by contact herbicides, to prevent overgrowth in rows and avoid competition for light, water and nutrients (Knight and Keep 1960; Lawson and Wiseman 1983). Primocane numbers are controlled for the following seasons cropping by pruning in winter and early spring to reduce inter-cane competition. Fruit is harvested annually from each plant, although both non-fruiting vegetative canes (primocanes) and fruiting canes (fructocanes) are present. The crop is usually supported on a post-and-wire system designed to carry the weight of fruits and to protect canes from excessive damage due to wind, harvesting and cultivation. Old dead fruiting canes must also be removed by pruning after harvest. Such pruning operations remove sources of fungal inoculum from the plantation and are important for the long-term health of the crop.

The emergence of Spotted Wing Drosophila in many growing regions worldwide now poses a real threat to raspberry and blackberry crops, and in California alone it has been calculated that losses of ca. $39.4 million can be attributed to this pest between 2009 and 2014 (Farnsworth et al. 2017). Removal of all fruit (including dropped or damaged berries) is now an important part of crop health management programmes (Raffle and Fountain 2017)

1.5 Genetic Diversity

Modern cultivars of raspberry and blackberry remain only a few generations removed from their wild progenitor species, but domestication has resulted in a reduction of both morphological and genetic diversity (Haskell 1960; Jennings 1988), with modern cultivars relatively homozygous compared to wild accessions and genetically similar to each other (Dale et al. 1993; Graham and McNicol 1995). The lack of genetic diversity is a serious concern for future *Rubus* breeding, especially when seeking durable host resistance to pests and diseases. The genetic base can be increased by the introduction of unselected raspberry clones and species material (Knight 1986), thus protecting biodiversity for future *Rubus* breeding programs, and such work is essential to enable breeders respond to future environmental challenges, changing growing conditions and emerging pest and disease problems. However, the time required to produce finished cultivars from unselected wild material can be considerable, particularly if several generations of backcrossing are required to remove undesirable traits.

A number of studies have been carried out to characterize the levels of genetic variation in wild species and to examine the turnover of wild populations. In Scotland, Graham et al. (1997, 2003) examined the spatial genetic diversity in wild accessions of red raspberry, and barriers to gene flow across geographic locations were detected, partly explained by a separation of flowering period, with altitude proving to be particularly important in this context (Marshall et al. 2001; Graham et al. 2003). Further studies at the same sites 10 years later by Graham et al. (2009b) found widespread reductions in plant numbers which, since each population had unique alleles, also equates to a loss of alleles, a finding with potentially serious long-term consequences for diversity.

Similar studies using phenotypic characteristics were carried out on wild raspberry populations in Russia (Ryabova 2007) and Lithuania (Patamsyte et al. 2004) In this study, soil acidity rather than geographic distance significantly correlated with polymorphisms indicating an environmental effect on diversity within populations.

Research on natural populations of other *Rubus* species have shown varying results; in *Rubus arcticus* populations genetic diversity was estimated at levels near 50% for among and within population estimates (Lindqvist-Kreuze et al. 2003). Diversity in wild populations of *R. moluccanus* L. in the Philippines was examined by Busemeyer et al. 1997, and the results were similar to that of Graham et al.

(1997, 2003), with greater similarity present within populations at each location than between locations. Genetic diversity has been examined in natural populations of black raspberry (*R. coreanus*) (Hong et al. 2003) and populations have also been evaluated for traits of importance for use in red and black raspberry breeding (Finn et al. 2003). A study on 63 natural populations of *Rubus strigosus* across North America (Marking 2006) found the majority of the variation to be within populations (79.5%). Weber (2003) analyzed genetic diversity in cultivars of black raspberry (*R. occidentalis*) and red raspberry and found that black raspberry genotypes showed on average 81% genetic similarity. 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. This compared well to the 70% similarity measured among red raspberry cultivars in Europe (Graham et al. 1995).

1.6 Genetic Resources

In the light of current climate change implications, collections of *Rubus* accessions from both wild and cultivated genepools represent a major resource for the development of new cultivars, better adapted to a changing natural environment. An example of this is the wild *Rubus* species collection held at the United States Department of Agriculture (USDA) Agricultural Research Service, National Clonal Germplasm Repository (Hummer and Finn 1999). Evaluation of this wild germplasm led to the identification of four sources of aphid resistance, two of which were introgressed into the elite breeding pool in two mapping populations (Bassil et al. 2014). A number of other major *Rubus* germplasm collections exist around the world, including at the Canadian Clonal Genebank (Luffman 1993), where over 140 accessions are maintained in a field collection and in protected culture, and in the UK where field collections of over 150 accessions exist at James Hutton Institute in Scotland and at East Malling Research in England (A. Dolan, pers. comm.). Collections from botanical surveys in Columbia consist of ten *Rubus* species recorded in open and/or disturbed habitats while plant material and seeds from exploration trips in Sakhalin territory are stored in gene banks including an orange *Rubus chamaemorus,* and a dark purple cloudberry (*R. pseudochamaemorus*) (Sabitov et al. 2007). In Europe, the 'GENBERRY' project (Denoyes-Rothan et al. 2008), was designed to ensure that agricultural biodiversity of small berries was preserved, characterized and used to improve varieties adapted to local European regions. The project focused on the construction of core collections, the development of a passport data list, the selection and definition of appropriate primary and secondary descriptors, characterization of genotypes using molecular markers, identification of health nutritional compounds and diseases evaluation for a large subset of the collections and the establishment of the European small berries database sustained by a continuous long term network (Denoyes-Rothan et al. 2008). In addition to the formally recognised collections, most breeders and their institutions retain a working germplasm collection that is accessed for parental material on a regular basis.

1.7 Breeding and Cultivar Development

In recent years the *Rubus* industry has relied on a small number of cultivars, often with limited pest and disease resistance, due to consumer and multiple retailer preferences, but at the same time the number of pesticides available for crop protection is decreasing. Additionally, consumers are increasingly concerned about the methods and environmental footprint of food production, and retailers are responding by requiring continued reduction in agricultural inputs and increased sustainability of local production. Conventional breeding has produced significantly enhanced cultivars (Finn and Hancock 2008), but progress in meeting the new challenges in today's marketplace can be slow in these highly heterozygous out-breeders. Selection of superior genotypes requires many years of assessment and evaluation, to ensure that new cultivars can deliver suitable quality in a sustainable way in commercial situations. The status of breeding progress in both Europe and North America are discussed in this volume in Chap. 2.

Breeding programmes in the various growing regions worldwide share common as well as specific goals, influenced by environmental conditions and challenges, end user requirements and available germplasm as well as financial and other resources. However, yield, fruit quality, abiotic and biotic stress tolerance, and ease of pick are key objectives for most programmes.

Fruit quality can be subdivided into physical quality, which includes berry size and shelf-life, and compositional quality. For physical quality, the size of berry is a key objective in many breeding programmes, as this trait can have a significant impact on the cost of harvest. Shelf-life and fruit softening also significantly impact costs in production due to losses on farm and also rejects from retailers. Fruit softening is an important agronomical trait that involves a complex interaction of plant cell processes. Recently QTLs were located primarily on linkage group (LG) 3 with other significant loci on LG 1 and LG 5 of the Latham x Glen Moy map (Simpson et al. 2017). The expression of key genes that underlie these QTLs, with roles in cell wall solubility, water uptake, polyamine synthesis, transcription and cell respiration were tested and gene expression patterns showed variable expression patterns across fruit development with highly significant positive and negative correlation between genes, supporting precise regulation of expression of different cell processes throughout raspberry fruit development.

Rubus berries have some of the highest levels of antioxidants and phytonutrients of any fruit crop, due primarily to their intense concentration of anthocyanins and phenolic compounds (Moyer et al. 2002). This has led to a number of investigations on antioxidant levels of raspberries (eg. Moore et al. 2008; Weber et al. 2008). A review of the chemical, sensory and health benefits of *Rubus* fruits is given by Hancock and McDougall in this volume.

Two of the main drivers of changing priorities and methodologies in *Rubus* breeding are the move towards primocane cultivars and the adoption of molecular breeding techniques (see Chaps. 2 and 8). In the case of primocane cultivars of raspberry, these offer the potential to extend the cropping season, reduce labour