Raspberry Breeding

Julie Graham and Nikki Jennings

1 World Production

Raspberries are grown in many parts of the world with production estimated at 482,763 MT (in 2005) (http:/ FAOSTAT.FAO.ORG). Europe is estimated to produce around half of all production (*Rubus idaeus* L.). This is an important high-value horticultural industry in many European countries, providing employment directly in agriculture, and indirectly in food processing and confectionary. Most raspberry production is concentrated in the northern and central European countries, although there is an increasing interest in growing cane fruits in southern Europe, for example, in Greece, Italy, Portugal and Spain. In many production areas, the fruit is grown for the fresh market, but in central Europe, for example, Poland, Hungary and Serbia, a high proportion of the crop is destined for processing. Major regions of production in North America include the Pacific North-West, California, Texas and Arkansas, as well as regions in New York, Michigan, Pennsylvania and Ohio. Chile, Argentina and Guatemala also have extensive production.

In Europe in particular, there has been increased interest in sales of raspberry fruits harvested from 'organic production'—farming based on methods relying entirely on crop rotation and avoidance of pesticide application (except certain substances currently permitted by the national regulatory authority for organic farming). However, with woody perennial crops, the difficulties of maintaining healthy productive plantations over many years are profound and it is too early to judge the overall success of these ventures in *Rubus* cane fruits. Increasing popularity of autumn-fruiting raspberries, in which late-season fruit is harvested from berries forming on the upper nodes of primocanes (Jennings and Brennan 2002), has extended the production season and the period of attack of some foliar and cane pests. Some very early spring fruits with high value can also be obtained from the remaining lower nodes of these over-wintered

J. Graham
Scottish Crop Research Institute, Invergowrie, Dundee DD2 5DA, UK
e-mail: Julie.Graham@SCRI.AC.UK.

S.M. Jain, P.M. Priyadarshan (eds.), *Breeding Plantation Tree Crops: Temperate Species*, DOI: 10.1007/978-0-387-71203-1_7,

primocane-fruiting types. Primocane-fruiting raspberries tend to be grown in the warmer areas of Europe where the temperature in autumn is relatively high and there is little risk of early autumn frosts. Interest has also been shown in extended-season production under glass or plastic structures in northern European countries, for example, Belgium (Meesters and Pitsioudis 1993; Verlinden 1995) and the UK (Barry 1995), and now in the Mediterranean fringe, for example, Spain and Greece, and this trend will affect their pest and disease status. To satisfy these production systems, long primocanes grown in northern regions, such as Scotland, are lifted, chilled and stored for long periods for planting in late spring for late summer harvest under plastic. The concept of extended-season production has been so successful that by careful manipulation of plant dormancy cycle and flower initiation, it is now possible to produce fresh raspberries in Europe for sale in almost all months.

Fruit has become important in the human diet due to increased consumers' awareness of healthy eating practices. In 2003, the global fresh fruit market was valued at £7.6 billion at current prices, having increased by just 3.9% since 1999. The fresh fruit sector accounts for 38.1% of the overall market and is gaining share due to continuing trend towards convenience food. Banana account the largest segment of the fruit sector with 22.5% of the market in 2003.

In terms of soft fruits, strawberries remain the best-selling soft fruit, but other fruits such as raspberry are gaining popularities because the increasing all-year round availability. Raspberries have always been attractive as fresh dessert fruits or for processing from frozen berries into conserves, purees and juices. It is interesting to see that raspberries were first used in Europe for medicinal purposes (Jennings 1988), but there is now heightened interest focused on these foods as major sources of antioxidants, such as anthocyanins, catechins, flavonols, flavones and ascorbic acid, compounds that protect against a wide variety of human diseases, particularly cardiovascular disease and epithelial (but not hormone-related) cancers (Deighton et al. 2000; Moyer et al. 2002). As a result, the consumption of these berries is expected to increase substantially in the near future as their value in the daily diet is publicised. A concerted effort by the public health authorities in Finland, for example, has promoted the consumption of small berry fruits to their populations (Puska et al. 1990) and in 2002, a similar initiative was launched in Scotland (Berry Scotland Project www.berry-scotland.com), though success here has yet to be demonstrated.

2 Raspberry Botany

Raspberries belong to the genus *Rubus*, one of the most diverse in the plant kingdom, comprised of a highly heterozygous series of some 500 species with ploidy levels ranging from diploid to dodecaploid (Jennings, 1988; Meng and Finn 2002). Members of the genus can be difficult to classify into distinct species for a number of reasons including hybridisation between species and apomixes

Fig. 1 (**A**) Red raspberry; (**B**) black raspberry; (**C**) protected crop of Glen Dell and (**D**) effect of root rot on field-grown plants (*See* color insert)

(Robertson 1974). These domesticated subgenera contain the raspberries, blackberries, arctic fruits and flowering raspberries, all of which have been utilised in breeding programmes. The most important raspberries are the European red raspberry (Fig. 1A), *R. idaeus* L. subsp. *idaeus*, the North American red raspberry *R. idaeus* subsp. strigosus Michx and the black raspberry (*R. occidentalis* L.) (Fig. 1B). *Rubus* subgenus *Idaeobatus* is distributed principally in Asia but also in East and South Africa, Europe and North America. In contrast, subgenus *Eubatus* is mainly distributed in South America, Europe and North America (Jennings 1988). The members of subgenus *Idaeobatus* spp. are distinguished by the ability of their mature fruits to separate from the receptacle. (For a list of *Rubus* species, subgenera and sections, see Skirvin et al. 2005.)

Details of the growth cycle of raspberry have been described by Jennings 1988). Raspberries are woody perennial plants with a biennial cane habit (Hudson 1959). Fruit is harvested annually from each plant, although both non-fruiting vegetative canes (primocanes) and fruiting canes (fructocanes) are present. This main season summer-fruiting 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. Primocanes are produced in numbers excessive to requirements for cropping in the following season; so many must be removed by pruning in winter and early spring to reduce inter-cane competition and create an open crop canopy for efficient light capture. 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.

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. Raspberries produce copious amount of nectar and attract bees. 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. Raspberries are an aggregate fruit, composed of individual drupelets, held together by almost invisible hairs. The one-seeded drupelets are set together on a small conical core (Jennings 1988). In *Rubus*, each carpel will develop into a small drupelet, with the mesocarp becoming fleshy and the endorcarp becoming hard and forming a tiny pit that encloses a single seed. Each drupelet usually has a single seed, though a few have two. Fruiting begins in the second year of planting, and in favourable conditions plantations can continue to fruit for more than 15 years. Fruit development occurs rapidly, taking only 30–36 days for most raspberry cultivars.

Primocanes and fruiting canes are in close proximity resulting in a complex plant architecture that provides spatial and temporal continuity for pests and pathogens to colonise a range of habitats (Willmer et al. 1986). The complex nature of the plant architecture also creates a barrier of foliage that impedes spray penetration of plant protectant chemicals, thus requiring specialised chemical application equipment (Gordon and Williamson 1988). Healthy plantations are expected to crop productively for more than 10 years, but this is only possible if the planting stocks and soils are free from persistent viral, bacterial and fungal diseases and certain pests, and hence the importance of quarantine arrangements and certification schemes to protect the propagation industry and fruit production (Jones 1991; Smith 2003).

Raspberry roots spread completely across the inter-row space, and these young canes (‘suckers’) developed from root buds (Hudson 1959; Knight and Keep 1960) must be removed, mechanically by tractor-mounted flailing equipment or by contact herbicides, to prevent competition of these suckers for light, water and nutrients with the crop.

3 Genetic Resources

Roach (1985) and Jennings (1988) gave accounts of the early domestication of red raspberry (*R. idaeus* L). During the 19th century, the North American red raspberry (*R. idaeus* subsp. strigosus Michx) was introduced in Europe and subsequently crossed with the European sub-species (R. *idaeus* subsp. vulgatus Arrhen.). Five parent cultivars dominate the ancestry of red raspberry—'Lloyd George' and 'Pynes Royal' entirely derived from *R. idaeus* var. vulgatus and 'Preussen', 'Cuthbert' and 'Newburgh' derived from both the sub-species. Controlled crossing began slightly earlier in the USA than the UK with the introduction of Latham in 1914 (McNicol and Graham 1992). Domestication has resulted in a reduction of both morphological and genetic diversity in red raspberry (Graham et al. 1996; Haskell 1960; Jennings 1988) with modern cultivars being genetically similar (Dale et al. 1993; Graham and McNicol 1995). This restricted genetic diversity is of serious concern for future *Rubus* breeding, especially when seeking durable host resistance to intractable pests and diseases for which the repeated use of pesticides in some regions is ineffective, unsustainable or unacceptable for certain selected markets, such as 'organic production'. The gene base can and is being increased by the introduction of unselected raspberry clones and species material (Knight et al. 1989). The time required to produce finished cultivars from this material, however, can be considerable particularly if several generations of back-crossing are required to remove undesirable traits.

There are 30 *Rubus* breeding programmes in 19 countries, almost all of which are in Europe or North America. The Scottish bred cultivar 'Glen Ample', released in the mid-1990s, now dominates the UK market (www.fruitgateway.co.uk), superceding older varieties such as 'Malling Jewel', 'Glen Clova', 'Glen Prosen' and 'Glen Moy'. Glen Ample along with 'Tulameen' and recently the new cultivar 'Octavia' dominate the UK market and acreage due to their desirable fresh market characteristics. Serbia is a major world producer and exporter of raspberries, producing one quarter of the world tonnage. Ninety percent of the acreage is dominated by the North American cultivar 'Willamette'.

In recent years, consumer demand for fresh raspberries outwith the main production season has increased with high premiums being paid for fresh market raspberries. This demand is being met by imports from countries such as Spain, Portugal and Chile. Production of raspberries in either side of the main season is achieved through protected cropping under polytunnels (Fig. 1C), or glass, using novel systems of production to manipulate flowering and fruiting. Protected cropping and out of season production in European countries is expanding so that in areas of southern Spain, nearly 100% of fresh market raspberries are being grown under tunnels. The early season cultivar 'Glen Lyon' has a low chilling requirement, which makes it suitable for re-propagation and manipulation of canes and is currently the ideal variety for this production system.

These protected cropping systems have been adopted by the UK industry to improve fruit quality and extend the season. Since the majority of fresh market production goes to large supermarket chains, the demand for good fruit quality, flavour and shelf life is high. In other European countries, Pacific

Northwest-bred cultivars have led the industry, such as ‘Meeker’, ‘Willamette’ and ‘Tulameen’. Primocane-fruiting cultivar ‘Heritage’ has led the industry in many countries. In Scandanavia, the hardy Norwegian variety ‘Veten’ has been the mainstay for many years; now ‘Glen Ample’ has taken the lead.

In the USA, ‘Meeker’ and ‘Willamette’ developed in the mid-1900s are the primary cultivars, although recent publicly developed cultivars ‘Cowichan’ and ‘Coho’ are being widely planted. Black raspberry (*R. occidentalis* L.) production has traditionally been concentrated almost completely in Oregon, ‘Munger’ and ‘Jewel’ being the leading varieties; however, a strong South Korean industry has developed over the past 5 years.

4 Breeding Principals and Objectives

Rubus breeding is hampered by several genetic problems including polyploidy, apomixes, pollen incompatibility and poor seedling germination. The highly heterozygous nature of the germplasm requires evaluation of large seedling populations. Breeding is based on a generation-by-generation improvement in breeding stock through selection and intermating individuals showing promise of producing superior progeny. This average improvement in the progeny of breeding stock resulting from intermating selected parents is called response to selection. (For a review, see Hansche 1983).

A survey in 2000 indicated that there are around 30 *Rubus* breeding programmes in 19 different countries, mainly in Europe and North America. Breeding programmes sponsored by end-users or government-funded programmes aim to develop appropriate germplasm enabling their particular industry to realize its potential, and thus goals vary from programme to programme. Many are faced with the same challenges, however, as the industry requires cultivars with excellent quality, higher yield, greater pathogen resistance and adaptation. As new problems arise and new production systems are developed, breeding programmes are faced with meeting these demands with new cultivars. The core primary objectives in raspberry-breeding programmes include high-quality fruit, good yield, shelf life and suitability for shipping, if for the fresh market, suitability for mechanical harvesting for the processing market, adaptation to the local environment and improved pathogen resistance. Future changes in environmental, cultural and agronomic practices within the industry will impact strongly on both the nature of the germplasm required for the future and also the likely pest and disease problems.

Fruit quality must always be the major objective of any fruit-breeding programme. While many characteristics are important in the successful acceptance of new cultivars, fruit quality must be considered the premier factor. Flavour, appearance and shelf life are the main attributes of fresh market quality. Flavour is a highly subjective trait but can be broken down into multiple descriptors for taste, texture and other sensory characteristics. Good, acceptable raspberry flavour tends to be fruity, sweet and floral with some acidity and no bitterness (Harrison et al. 1999). Colour, brightness, size and shape contribute to appearance. A naturally dark colour can be perceived as overripe by fresh market retailers, whereas a darker colour is desirable for processing. Large size is an attractive characteristic to both consumers and producers as it is more cost-effective to pick.

The biennial cropping habit of raspberry means that both fruiting and vegetative canes exist together. Plant habit is important in plantation management and has a major effect on yield potential. In summer-fruiting types, the most important plant characteristics include number and height of young cane, consistency of bud break, internode length and lateral length and position. In primocane-fruiting types, the amount of branching and extent of lateral development on the primocanes are major yield components. In both types erect, spineless canes are desirable.

Machine harvesting for processing raspberries is the standard practice for most major raspberry production regions around the world and is essential where picking labour is expensive or unavailable. Despite advances in machine technology, it appears that the major improvements in harvesting will come from plant breeding (Cormack 1989). No single attribute has been found to determine successful machine harvest –ability, but a range of interacting traits governs harvest performance. A suitable genotype must have uniform strong vigour and good cane density with an upright habit. Medium-length laterals with good fruit presentation are also desirable. Maturity, physical shape of the berry and receptacle all contribute to ease of pick. This will help ensure that a high percentage of uniform, ripe fruit with acceptable process quality and minimal green fruit are harvested throughout the season (Hall et al. 2002).

In the UK and Europe, a transformation in cultivation practices has occurred from outside-field plantations to protected cropping systems. Such changes in agronomic practices affect plant growth, seasonality and fruit quality and have implications for a shift in pest and pathogen pressures. For example, in Scotland, pests such as two-spot spider mite (*Tetranychus urticae*) and diseases such as powdery mildew (*Sphaerotheca macularis*) are not a problem in field plantations but occur readily in tunnel production systems. Recently, breeding programmes in the UK have responded to this change in production by trialling and selecting germplasm under protected cropping systems. This will help to identify suitably adapted germplasm for commercial trialling and eliminate the most susceptible seedlings early in the breeding process.

While fruit quality must remain the priority in any commercial breeding programme, the incorporation of novel resistance/tolerance to pests and diseases is regarded as essential for the development of cultivars suitable for culture under integrated pest management (IPM) systems. Sources of resistance in diverse *Rubus* spp. to many pests and diseases have been identified and exploited in conventional cross-breeding (Keep et al. 1977; Jones et al. 1984; Jennings 1988; Knight 1991; Williamson and Jennings 1992). However, germplasm bearing single-resistance genes, when planted over extensive areas, can eventually be overcome by the rapid evolution of new biotypes of pests so that new types of host resistance are required to sustain plant protection (Birch et al. 2002; Jones et al. 2002).

Pest and diseases of raspberry in Europe have been extensively reviewed in Gordon et al. (2006). Major pest and diseases will be briefly discussed. Root rot, cane diseases and raspberry bushy dwarf virus (RBDV) are problems worldwide with aphids, cane midge and beetles being serious problems in Europe.

Root rot diseases have always been a problem in North America but were not regarded as a problem in Europe until the 1980s when *Phytophthora* root rot emerged as a major problem of raspberry with outbreaks in the UK (Duncan et al. 1987), Scandinavia and Germany (Seemüller et al. 1986) (Fig. 1D). Raspberry root rot became a serious problem throughout temperate Australia during the unusually wet years of 1994–1996 with *Phytophthora fragariae* var. *rubi* (Wilcox et al. 1993) identified as the major causal agent. This disease is now the most destructive disease of raspberries. Affected canes die in the first year of growth or their buds fail to emerge at the start of the second growing season. Alternatively, emerged laterals wilt and die at any time from emergence until late in fruiting. The almost simultaneous outbreaks of a new disease across Europe in traditional raspberry-growing areas (e.g., raspberries have been grown in Tayside, Scotland for more than century) suggested that the disease had spread through the propagation network and had been distributed to farms in new planting materials. Introduction of new and highly susceptible cultivars sought vigorously by industry was a major factor in disease spread.

The prevention of new outbreaks must become the underpinning philosophy in control strategies for root rot. Ensuring that the planting material is free of disease is most effective strategy. The pathogen is unlikely to be present widely in soil where raspberries have never been grown previously. Screening cultivars of red and other raspberries and wild *Rubus* species have identified potential sources of resistance. 'Latham' and 'Winkler's Sämling' were identified early as having significant resistance. Species material, such as *R. strigosus* and *R. ursinus*, have also been identified. Genetic resistance through plant breeding offers a feasible and effective method of control, but because of the time involved in combining resistance with other desirable traits, e.g., fruit size and quality, it has not yet had the anticipated impact in commercial production. More research to find resistance genes and breeding is required, especially marker-assisted breeding. Future breeding plans with respect to root rot resistance are underpinned by attempts to develop molecular markers linked to resistance to improve and accelerate selection efficiencies (Graham and Smith 2002). It seems likely that this potent disease will be managed most effectively in the future by enhanced host resistance.

Botrytis cinerea accounts for severe losses in yield in most seasons and can cause devastating losses post-harvest if control measures are inadequate, especially in regions with moderate rainfall during blossom and harvest. This pathogen is difficult to control because there are multiple infection sites and no strongly resistant cultivars available to growers. Unfortunately, conventional breeding has yet to produce cultivars that are highly resistant to grey mould, although there are some cultivars and selections with high levels of resistance to cane botrytis (Williamson and Jennings 1992). However, considerable variation in resistance to botrytis fruit rot has been reported in *R. crataegifolius* and *R. occidentalis*. Resistance to cane botrytis has recently been mapped and association with gene *H* conferring cane pubescence confirmed (Graham et al. 2006).

RBDV is the most common virus of *Rubus* worldwide (Martin 2002). This is of greatest concern in North America, particularly in the Pacific Northwest where the virus has reached epidemic proportions, probably due to the planting of newer cultivars that lack resistance. RBDV is a pollen-borne virus, which may cause a crumbly fruit symptom with foliar symptoms ranging from none to a bright yellow chlorosis, and in a few cultivars, there is a stunting of the plants. Not all infected plants show crumbly fruit. In black raspberry, RBDV does not cause significant fruit losses or symptoms but can reduce cane number and vigour. Since the virus cannot be controlled with chemical applications, the best means of controlling RBDV is with the use of immune cultivars; however, the occurrence of resistance-breaking isolates (RB) poses serious risks for future control.

The large raspberry aphid (*Amphorophora idaei*) is the most important aphid species found on raspberry in northern Europe causing direct feeding damage to susceptible cultivars (Fig. 2), but its major importance is as a vector of raspberry viruses that cause serious decreases in plant vigour (Jones 1986; Birch and Jones 1988). Raspberry cultivars containing genes for resistance to the large raspberry aphid have been in commercial use in the UK for more than

Fig. 2 Large raspberry aphid (*See* color insert)

40 years (Briggs 1965). The resistance largely depends on two single major genes that control aphid numbers and subsequently the spread of the viruses they transmit (Jones 1986). Unfortunately, virulent biotypes of *A. idaei* that can break these specific resistance genes in their raspberry host plants have now developed (Birch et al.1994; Birch et al. 2002).

The raspberry beetle (*Byturus tomentosus* De Geer) is a major pest of cultivated raspberry and hybrid berries in many countries of Europe and frequently found in fruits of wild raspberries and blackberries. Adult beetles can damage the buds and flowers by feeding on them in the spring and early summer, but the most important damage in Europe is caused by larvae. They browse on the surface of drupelets on the developing fruit resulting in discoloured or contaminated ripe fruit leading to rejection or down-grading of the crop. This damaged fruit can become infected by botrytis (*B. cinerea*), thus further reducing the storage of the ripe fruit (Woodford et al. 2002). Wild *Rubus* species, including *R. coreanus*, *R. craetigifolius, R. occidentalis* and *R. phoenicolaesius*, have been used as sources of resistance to raspberry beetle (Briggs et al. 1982) in breeding programmes. As yet, no commercial cultivars are available. Little is known about the mechanism(s) of resistance to raspberry beetle involved in wild *Rubus* species or crosses derived from them.

Feeding damage caused by raspberry cane midge (*Resseliella theobaldi*) larvae predisposes raspberry canes to the disease known as 'midge blight', which is responsible for major losses in raspberry in many parts of Europe (Woodford and Gordon 1978). In most of Europe, midge larvae only colonise splits in the bark of primocanes, but in Scandinavia, larvae have been reported from splits in fruiting canes of the cultivars 'Veten' (Sorum and Stenseth. 1988) and 'Ottawa' (Dalman 1991). The raspberry cv. Glen Prosen and the hybrid berries Tayberry and Loganberry do not readily split their rind in the spring, and are rarely affected by 'midge blight' because female midges are unable to find suitable oviposition sites unless they are caused by mechanical means. Other *Rubus* species and crosses have been investigated as sources of resistance to raspberry cane midge. *R. parviflorus, R. odoratus* and F_2 crosses of *R. crataegifolius* × *R. idaeus* were found to be resistant when exposed to raspberry cane midges.

5 Breeding Techniques

Breeding in raspberry is carried out by hybridisations between cultivars and/or species with desirable characteristics for multiple generations. Each cycle of crossing involves a cycle of greenhouse screening and field observation. Crosses tend to be done outwith the normal flowering period requiring dormant plants to be dug in autumn and placed in cold storage for around 6–10 weeks. The plants are then moved into an insect-proof greenhouse where the temperature is raised gradually from 10°C to 20°C over a 3-week period. Day length is set at 16 h. Plants break bud, produce laterals and begin to flower approximately 4 weeks later. Open flowers are collected into a Petri dish for use as a pollen source, dried at room temperature and stored with a desiccant at 4°C. Closed flower buds are emasculated with a scalpel and are ready to pollinate once the stigma have become receptive (approx. 48 h after emasculation). The pistil is pollinated with an artist's paintbrush. All tools and hands are sterilised with absolute alcohol between crosses, and all excess flower buds are removed to minimise pollen transfer in the greenhouse environment; therefore pollen bags are not required. Parent plants are sprayed for pests and diseases as appropriate for the duration of crossing.

Fruit from each family is collected when ripe and left in a pectinase solution overnight at room temperature. The pulp is separated from the seed by blending the mixture for 10 s in a domestic blender. The mixture is left to settle for 1 min; viable seed will sink to the bottom and pulp and non-viable seed will float to the top. The pulp is decanted from the viable seed. The seed is rinsed by filling the jug with tap water, leaving to settle and decanted. The rinse cycle is repeated three times, until the tap water is clear. The seed, which is clean and free of any pulp, is left to dry overnight on filter paper. Dry seed are stored in glassine bags (100 × 70 mm) with a desicant at 4°C.

Up to 1000 seed/family are scarified in acid, assuming 15–20% germination. Remaining seeds are stored in case of poor germination. Seed must be clean and dry before scarification in acid. Seed is transferred to a boiling tube (~500 seed/tube) with concentrated sulphuric acid for exactly 20 min and rinsed by pouring the seed and acid through a metal sieve, secured by a retort stand, and rinsing with tap water for 10 min. Seed should be submerged under the water during this period. Seed is then submerged in calcium hypochlorite solution for 6–10 days with stirring every day, and the solution should be changed once during this period. Once the seed coat has been scarified with acid, it is important that the seed is not left to dry out. Seed is rinsed under tap water for 10 min and mixed with damp vermiculite. The mixture is stored in a sealable bag at 4°C for 6 weeks. After this period, the seed and vermiculite is treated with GA_3 (3 ppm) and left at room temperature overnight.

The seed and vermiculite is sown onto Bulrush Brown/Black peat in a seed tray and covered with a fine layer of dry vermiculite. The trays are incubated at 20°C. Seeds should begin to germinate within 7 days.

6 Molecular Markers in Breeding

Breeding methods used in raspberry have changed very little over the last 40 years or so. Little novel germplasm has made its way into commercial cultivars. However, with the narrowing genetic base coupled with the increasing demands from consumers, new breeding methods are required to meet demands. The speed and precision of breeding can be improved by the deployment of molecular tools for germplasm assessment and the development of genetic linkage maps. The development and application of molecular markers have been reviewed by Antonius-Klemola (1999), Hokanson (2001) and Skirvin et al. (2005). The development of SSR markers (Graham et al. 2002; Stafne et al. 2005) has allowed the development of a raspberry genetic linkage map. This facilitates the development of diagnostic markers for polygenic traits and the identification of genes controlling complex phenotypes. Understanding the genetic control of commercially and nutritionally important traits and the linkage of these characteristics to molecular markers on chromosomes is the future of plant breeding. Red raspberry (*R. idaeus*) is a good species for the application of such techniques, being diploid ($2n = 2x = 14$) with a very small genome (275 Mbp). Indeed, the haploid genome size of raspberry is only twice the size of *Arabidopsis*, making it highly amenable to complete physical map construction, thereby providing a platform for map-based gene cloning and comparative mapping with other members of the Rosaceae (Dirlewanger et al. 2004). The availability of abundant genetic variation in natural and experimental populations and adaptation to a range of diverse habitats (Graham et al. 1997; Marshall et al. 2001; Graham et al. 2003) offers researchers a rich source of variation in morphology, anatomy, physiology, phenology and response to a range of biotic and abiotic stress. The ability to vegetatively propagated individual plants provides opportunities to capture genetic variation over generations and replicate individual genotypes to partition and quantify environmental and genetic components of variation of genetic linkage maps. These are necessary to develop diagnostic markers for polygenic traits and, in the future, possibly identify the genes behind the traits. The first genetic linkage of raspberry has recently been constructed (Graham et al. 2004). This 789 cM genetic linkage map was constructed utilising a cross between the phenotypically diverse European red raspberry cultivar Glen Moy and the North American cultivar Latham. SSR markers were developed from both genomic and cDNA libraries from Glen Moy. These SSRs, together with AFLP markers, were utilised to create a linkage map. An enhanced map with further SSR and EST-SSR and gene markers has recently been completed (Graham et al. 2006). This work has highlighted the importance of maps and markers with demonstration of the tight association between gene *H* and resistance to cane botrytis and spur blight (Graham et al. 2006).

7 Problems and Unknowns

For some breeding objectives, a lack of appropriate germplasm may seriously hamper progress. In these cases, genetic manipulation may be the way forward (Graham et al. 1996). This may not be possible in Europe in the near future, however, due to strong opposition from certain groups and sectors. Genetic manipulation in *Rubus* has been reviewed by Skirvin et al. (2005).

Most commercial raspberries are now maintained, propagated and sold as disease-indexed plants using micropropagation. Estimates of somaclonal variation of 1–3% per generation may be conservative with other estimates of 10% (Larkin et al. 1989).

References

Antonius-Klemola, K. (1999). Molecular markers in *Rubus* (Rosaceae) research and breeding. *Journal of Horticultural Science and Biotechnology* **74**:149–160.

Barry, N. (1995). Extending and consolidating the UK soft fruit season with French tunnels. In: Proceedings of the ADAS/HRI Soft Fruit Conference 1995 – New Developments in the Soft fruit Industry. Ashford, Kent. pp. 63–68.

Birch, A.N.E. and Jones, A.T. (1988). Levels and components of resistance to *Amphorophora idaei* in raspberry cultivars containing different resistance genes. *Annals of Applied Biology* **113**:567–578.

Birch, A.N.E., Fenton, B., Malloch, G., Jones, A.T., Phillips, M.S., Harrower, B.E., Woodford, J.A.T. and Catley, M.A. (1994). Ribosomal spacer variability in the large raspberry aphid, *Amphorophora idaei* (Aphidinae: Macrosiphini). *Insect Molecular Biology* **3**:229–245.

Birch, A.N.E., Jones, A.T., Fenton, B., Malloch, G., Geoghegan, I., Gordon, S.C., Hillier, J. and Begg, G. (2002). Resistance-breaking raspberry aphid biotypes: Constraints to sustainable control through plant breeding. *Acta Horticulturae* **587**:315–317.

Briggs, J.B. (1965). The distribution, abundance and genetic relationships of four strains of *Rubus* aphid (*Amphorophora rubi*) in relation to raspberry breeding. *Journal of Horticultural Science* **40**:109–117.

Briggs, J.B., Danek, J., Lyth, M. and Keep, E. (1982). Resistance to the raspberry beetle, *Byturus tomentosus*, in *Rubus* species and their hybrid derivatives with *R. idaeus*. *Journal of Horticultural Science* **57**:73–78.

Cormack, M.R. (1989). Growers and processors set to meet the challenge. *Grower* November 19.

Dale, A., Moore, P.P., McNicol, R.J., Sjulin, T.M. and Burmistrov, L.A. (1993). Genetic diversity of red raspberry varieties throughout the world. *Journal of the American Society of Horticultural Science* **118**:119–129.

Dalman, P. (1991) The effect of new cultivation practices on the yield, cane growth and health status of red raspberry (*Rubus idaeus* L.) in Finland. *Annales Agriculturae Fenniae* **30**:421–439.

Deighton, N., Brennan, R., Finn, C. and Davies, H.V. (2000). Antioxidant properties of domesticated and wild *Rubus* species. *Journal Science and Food Agriculture* **80**:1307–1313.

Dirlewanger, E., Graziano, E., Joobeur, T., Garriga-Caldere, F., Cosson, P., Howad, W. and Aris, P. (2004). Comparative mapping and marker-assisted selection in Rosaceae fruit crops. *Proceeding of the National Academy of Sciences USA* **101**:9891–9896.

Duncan, J.M., Kennedy, D.M. and Seemüller, E. (1987). Identities and pathogenicities of *Phytophthora* spp. causing root rot of red raspberry. *Plant Pathology* **36**:276–289.

Gordon, S.C. and Williamson, B. (1988). Comparison of an air-assisted cross-flow sprayer with conventional hydraulic sprayer for the control of raspberry aphids by fenitrothion. *Crop Protection* **7**:106–111.

Gordon, S.C., Williamson, B. and Graham J. (2006) Current and Future Control Strategies for Major Arthropod Pests and Fungal Diseases of Red Raspberry (*Rubus idaeus*) in Europe. In: CROPS: Growth, Quality and Biotechnology ed. Dris WFL Publisher, Finland 925–950.

Graham, J. and McNicol, R.J. (1995). An examination of the ability of RAPD markers to determine the relationships within and between *Rubus* species. *Theoretical and Applied Genetics* **90:**1128–1132.

Graham, J., Gordon, S.C. and Williamson, B. (1996). Progress towards the use of transgenic plants as an aid to control soft fruit pests and diseases. In: *Proceedings of Brighton Crop Protection Conference-Pests & Diseases* -1996. **3**:777–781.

Graham, J., Squire, G.R., Marshall, B. and Harrison, R.E. (1997). Spatially-dependent genetic diversity within and between colonies of wild raspberry *Rubus idaeus* detected using RAPD markers. *Molecular Ecology* **6:**272–281.

Graham, J., Smith, K., Woodhead, M. and Russell, J. (2002). Development and use of SSR markers in *Rubus* species. *Molecular Ecology Notes* **2:**250–252.

Graham, J. and Smith, K. (2002). DNA markers for use in raspberry breeding. *ActaHorticulture* **585**:51–56

Graham, J., Marshall, B. and Squire, G. (2003). Genetic differentiation over a spatial environmental gradient in wild *Rubus idaeus* populations. *New Phytologist* **157**: 667–675.

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

Graham, J., Smith, K., Tierney, I., MacKenzie, K. and Hackett, C.A. (2006). Mapping gene *H* controlling cane pubescence in raspberry and its association with resistance to cane botrytis and spur blight, rust and cane spot. *Theoretical and Applied Genetics* **112**:818–831.

Hall, H.K., Stephens, M.J., Alspach, P., Stanley, C.J. and Kempler, C. (2002). Traits of importance for machine harvest of raspberries. *Acta Hortculturae* **585**:607–610.

Hansche, P.E. (1983). Response to selection. In: Moore, J.N. and Janick, J. (eds.), Methods in Fruit Breeding. Purdue University Press, Indiana. pp. 154–171.

Harrison, R.E., Brennan, R.M., Hunter, E.A., Morel, S. and Muir, D.D. (1999). Genotypic, environmental and processing effects on the sensory character of *Rubus* and *Ribes*. *Acta Horticulturae* **505**:25–32.

Haskell, G. (1960). The raspberry wild in Britain. *Watsonia* **4**:238–255.

Hokanson, S.C. (2001). SNiPs, Chips, BACs and YACs: are small fruits part of the party mix? *HortScience* **36**:859–871

Hudson, J.P. (1959). Effects of environment on *Rubus idaeus* L. Morphology and development of the raspberry plant. *Journal of Horticultural Science* **34**:163–169.

Jennings, D.L. (1988). Raspberries and blackberries: their breeding, diseases and growth. London: Academic Press, 230 pp.

Jennings, S.N. and Brennan R.M. (2002). Improvement of raspberry cultivars in Scotland. *Acta Horticulturae* **585**:179–183.

Jones, A.T., Gordon, S.C. and Jennings, D.L. (1984). A leaf-blotch disorder of tayberry associated with the leaf and bud mite (*Phyllocoptes gracilis*) and some effects of three aphid-borne viruses. *Journal of Horticultural Science* **59**:523–528.

Jones, A.T. (1986). Advances in the study, detection and control of viruses and virus diseases of *Rubus*, with particular reference to the United Kingdom. *Crop Research* **26**:127–171.

Jones, A.T. (1991). The raspberry certification program in the United Kingdom. In: Ellis, M. A., Converse, R.H., Williamson, R.N. and Williamson, B. (eds.), Compendium of raspberry and blackberry diseases and insects St. Paul, Minnesota: APS Press, pp. 89–90.

Jones, A.T., McGavin, W.J. and Birch, A.N.E. (2002). Effectiveness of resistance genes to the large raspberry aphid, *Amphorophora idaei* Börner, in different raspberry (*Rubus idaeus* L.) genotypes and under different environmental conditions. *Annals of Applied Biology* **136**:147–152.

Keep, E., Knight, V.H. and Parker, J.H. (1977). *Rubus coreanus* as donor of resistance to cane diseases and mildew in red raspberry breeding. *Euphytica* **26**:505–510.

Knight, R.L. and Keep, E. (1960). The genetics of suckering and tip rooting in the raspberry. In: "Report of East Malling Research Station for 1959", UK. pp. 57–62

Knight, V.H., Jennings, D.L. and McNicol R.J. (1989). Progress in the UK raspberry programme. *Acta Horticulturae* **262:**93–103.

Knight, V.H. (1991). Use of salmonberry, *Rubus spectabilis* Pursh., in red raspberry breeding. *Journal of Horticultural Science* **66**:575–581.

Larkin, P.J., Banks, P.M., Bhati, R., Brettell, R.I.S., Davies, P.A., Ryan, S.A., Scowcroft, W. R., Spindler, L.H. and Tanner, G.J. (1989). From somatic variation to variant plants: mechanisms and applications. *Genome* **31:**705–711.

Marshall, B., Harrison, R.E., Graham, J., McNicol, J.W., Wright, G. and Squire, G.R. (2001). Spatial trends of phenotypic diversity between colonies of wild raspberry *Rubus idaeus*. *New Phytologist* **151:**671–682.

Martin, R.R. (2002). Virus diseases of *Rubus* and strategies for their control. *Acta Horticulturae* **585**:265–270.

McNicol, R.J. and Graham, J. (1992). Temperate small fruit **12**:303–321. In: Biotechnology of Perennial Fruit Crops eds. Hammerschlag and Litz.

Meesters, P. and Pitsioudis, A. (1993). Jaarrondteelt herfstframboos onder verwarmd glas (deel 2). *Fruitteelt* **6**:8–9.

Meng, R. and Finn, C.E. (2002). Determining ploidy level and nuclear DNA content in *Rubus* by flow cytometry. *Journal of the American Society for Horticultural Science* **127**:223–227.

Moyer, R.A., Hummer, K.E., Finn, C.E., Frei, B. and Wrolstad, R.E. (2002). Anthocyanins, phenolics,and antioxidant capacity in diverse small fruits: *Vaccinium*, *Rubus*, and *Ribes*. *Journal of Agri Food Chem* **50**:519–525.

Puska, P., Vartiainen, E., Korhonen, H.J., Kartovaara, L., Berg, M-A., Pietinen, A., Nissinen, P. and Tuomilehto, J. (1990). The North Karelia Project: results of a major national demonstration project on CHD prevention in Finland since 1972. *Atherosclerosis Rev* **21**:109–117.

Roach, F.A. (1985). Cultivated Fruits of Britain: Their Origin and History. Oxford: Blackwell.

Robertson, K.R. (1974). The genera Rosaceae in the southeastern United States. *Journal of the Arnold Arboretum* **55**:352–360.

Seemüller, E., Duncan, J.M., Kennedy, D.M. and Riedel, M. (1986). *Phytophthora* sp. als Ursache einer Wurzelfäule an Himbeere. *Nachrichenblatt des Deutschen Pflanzenschutzdienstes* **38**:17–21.

Skirvin, R.M., Motoike. S., Coyner, M. and Norton M.A. (2005). *Rubus* spp. Cane Fruit. In: Litz, R.E. (eds.), Biotechnology of Fruit and Nut Crops. CABI Publishing UK.

Smith, V.V. (2003). The role of certification schemes in integrated crop management of soft fruit in Scotland. *IOBC/wprs Bulletin* **26:**7–10.

Sorum, O. and Stenseth, C. (1988). Bringebaermoll (*Incurvaria rubiella*). *Gartneryrket* **78**:289.

Stafne, E.T., Clark, J.R., Weber, C.A., Graham, J. and Lewers, K. (2005) Simple sequence repeat (SSR) markers for genetic mapping of raspberry and blackberry. *Journal Amer Soc Horticultural Science* **130:**722–728

Verlinden, A. (1995). De telt van bramen onder glas in containers-RILLAAR 1994. *Fruitteelt Nieuws* **8**:22–23.

Willmer, P.G., Hughes, J.P., Woodford, J.A.T. and Gordon, S.C. (1986). The effects of crop microclimate and associated physiological constraints on the seasonal and diurnal distribution patterns of raspberry beetle (*Byturus tomentosus*) on the host plant *Rubus idaeus*. *Ecological Entomology* **21**:87–97.

Williamson, B. and Jennings, D.L. (1992). Resistance to cane and foliar diseases in red raspberry (*Rubus idaeus*) and related species. *Euphytica* **63**:59–70.

Wilcox, W.F., Scott, P. H., Hamm, P.B., Kennedy, D.M., Duncan, J.M., Brasier, C.M. and Hansen, E.M. (1993). Identity of a *Phytophthora* species attacking raspberry inEurope and North America. *Mycological Research* **97**:817–831.

Woodford, J.A.T. and Gordon, S.C. (1978). The history and distribution of raspberry cane midge (*Resseliella theobaldi* (Barnes) = *Thomasiniana theobaldi* Barnes), a new pest in Scotland. *Horticultural Research* **17**:87–97.

Woodford, J.A.T., Williamson, B. and Gordon, S.C. (2002). Raspberry beetle damage decreases shelf-life of raspberries also infected with *Botrytis cinerea*. *Acta Horticulturae* **585**:423–427.