HortScience 60(7):1180–1199. 2025. https://doi.org/10.21273/HORTSCI18571-25

Breeding for Resistance to Significant Disease and Insect Pests of Red and Black Raspberry (*Rubus idaeus* and *R. occidentalis*) in the Pacific Northwest

Savannah N. Phipps
Oregon State University, Department of Botany and Plant Pathology, 2701 SW Campus Way, Corvallis, OR 97331, USA

Nahla V. Bassil
US Department of Agriculture–Agricultural Research Service, National Clonal Germplasm Repository, 3347 Peoria Rd, Corvallis, OR 97333, USA

Jeffery A. DeLong
US Department of Agriculture–Agricultural Research Service, Horticultural Crops Disease and Pest Management Research Unit, Corvallis, OR 97330, USA

Wendy Hoashi-Erhardt
Washington State University, Puyallup Research and Extension Center, 2606 West Pioneer, Puyallup, WA 98371, USA

Jana Lee
US Department of Agriculture–Agricultural Research Service, Horticultural Crops Disease and Pest Management Research Unit, 3420 NW Orchard Ave, Corvallis, OR 97330, USA

Kelly J. Vining
Oregon State University, Department of Horticulture, 4017 Agricultural Life Sciences Building, Corvallis, OR 97331, USA

Jerry E. Weiland and Inga A. Zasasda
US Department of Agriculture–Agricultural Research Service, Horticultural Crops Disease and Pest Management Research Unit, 3420 NW Orchard Ave, Corvallis, OR 97330, USA

Michael A. Hardigan
US Department of Agriculture–Agricultural Research Service, Horticultural Crops Production and Genetic Improvement Research Unit, 3420 NW Orchard Ave, Corvallis, OR 97330, USA

Keywords. biotic stress resistance, genomics, pathogens, pests, phenomics, raspberry breeding

Abstract. **Developing cultivars that are resistant to multiple biotic stresses is an important objective in raspberry plant breeding. Diseases such as *Raspberry bushy dwarf virus* and Phytophthora root rot have long been a high priority for raspberry breeding programs, whereas other pests, such as spotted wing Drosophila and the root lesion nematode, have been considered more recently. Breeding for improved resistance to these stresses has relied primarily on conventional breeding methods. However, rapid technological progress and increased access and affordability of genomic and phenomic methodologies may accelerate breeding and improve selection efficiency for genetic resistance to pests and pathogens. Such advancements are understudied for application in raspberry, but are emerging as a significant research interest. We review the current state of plant breeding research for the most significant diseases and pests affecting raspberry production in the Pacific Northwest of North America. In addition, we discuss new and relevant plant breeding methodologies that could contribute to future breeding objectives.**

The Pacific Northwest (PNW) of North America encompasses the states of Washington, Oregon, Idaho, USA, and the Canadian province of British Columbia, where climate is heavily influenced by proximity to the Pacific Ocean. The PNW has a large diversity of crops, with more than 300 different agricultural commodities produced in Washington, USA alone (Washington State Department of Agriculture n.d.). The temperate climate and well-drained sandy loam soils of the PNW region make it well suited for caneberry production, which includes red raspberry (*Rubus idaeus* L.), black raspberry (*R. occidentalis* L.), and blackberry (*Rubus* spp.). As a result, Oregon and Washington are consistently ranked among the states with the highest raspberry yields and harvested area in the United States (Fig. 1). Although much of the fresh-market production of caneberries in North America occurs in California, USA, and Mexico, most of the processed market production of caneberries in the United States occurs in the PNW. Washington ranks first in the nation for processed red raspberry production, whereas Oregon is among the top five (Menzies 1999; Oregon Raspberry and Blackberry Commission n.d.). Oregon leads the United States in black raspberry production (Oregon Raspberry and Blackberry Commission n.d.).

The longevity of red raspberry plantings in this region is typically 6 to 7 years, but can be more than 12 years depending on the cultivar, cultural practices, and abiotic and biotic stresses (DeVetter et al. 2018; Hummer and Hall 2013). Of these, Phytophthora root rot (causal agent: *Phytophthora rubi*), the root lesion nematode (*Pratylenchus penetrans*), and *Raspberry bushy dwarf virus* (RBDV) are the most significant diseases reducing the life span of red raspberries throughout the region (Quito-Avila et al. 2014; Rudolph et al. 2019a; Weiland et al. 2018, 2024). Black raspberry is susceptible to common root rot pathogens and plant viruses, including Verticillium wilt (causal agent: *Verticillium dahliae*), RBDV, and *Strawberry necrotic shock virus*, and tends to last only 3 or 4 years before being removed as a result of reduced vigor, yield, and fruit quality caused by diseases (Halgren et al. 2007). Raspberry typically matures and becomes economically productive by the third year after planting, and growers want their plantings to be as long-lived as possible to reduce replanting costs, which were $5597/acre for red raspberry in 2015 (Galinato and DeVetter 2016). Between economic and environmental pressures, PNW breeders strive to release elite raspberry cultivars that withstand significant disease pressures such as the ones mentioned here.

Within the past few decades there has been significant progress in the development and accessibility of genomic and phenomic technologies for agriculture. These new tools can increase the selection efficiency for developing and identifying improved cultivars. Although these methods can be applied to most crops, they are particularly valuable for breeding programs focused on woody perennial crops with long cultivar development cycles such as raspberries. These methods present the opportunity to achieve the goal of improving biotic stress resistance in raspberries and are currently being evaluated by programs around the world. Here, prevalent pests and diseases important to PNW breeding programs are discussed, as well as current genetic and phenomic efforts to understand more fully and breed for those stresses.

Raspberry Breeding in the PNW

Raspberries are increasingly popular with consumers because they contain nutraceutical compounds with anticarcinogenic and anti-inflammatory effects (Jean-Gilles et al. 2012; Mace et al. 2014; Montrose et al. 2011; Rodrigo et al. 2006; Shi et al. 2016, 2017). The steady increase in global production and acreage planted in recent decades reflects increasing consumer demand (Fig. 2). In 2021, the top five raspberry-producing countries were Russia, Mexico, Serbia, Poland, and the United States (Food and Agriculture Organization of the United Nations n.d.) (Table 1). With increasing consumer demand, there is greater pressure to develop cultivars with higher fruit quality and yields, resistance to common pests and pathogens, and improved machine harvestability to offset challenges related to the cost and availability of labor.

Caneberry breeding in the PNW has been led by the US Department of Agriculture (USDA)–Agricultural Research Service (ARS) Horticultural Crops Production and Genetic Improvement Research Unit (HCPGIRU; formerly, the USDA-ARS Horticultural Crops Research Unit) (Corvallis, OR, USA), the Washington State University (WSU) Small Fruit Breeding program (Puyallup, WA, USA), and British Columbia Berry Cultivar Development Inc. (BCBCDI) (Abbotsford, BC, Canada). Historically, Agriculture and Agri-Foods Canada (AAFC) partnered with Pacific Agri-Food Research Centre (PARC) for raspberry breeding, but now collaborates with the BCBCDI. The USDA-ARS program in Oregon was started in 1928 and is one of the oldest blackberry and raspberry breeding programs in the United States (Finn and Clark 2012). The WSU program was started soon after in 1929, followed by the AAFC-PARC program in British Columbia, Canada, in the 1950s (Jennings 2018; Moore and Hoashi-Erhardt 2016). Since their inception, these programs have worked collaboratively to meet the needs of PNW growers. In the private sector, Northwest Plant Co./Pacific Berries, LLC (Ferndale, WA, USA), and The New Zealand Institute for Plant and Food Research Ltd. (Mt. Albert, Auckland, NZ) have cooperatively developed and released raspberry cultivars, as has Driscoll's (Watsonville, CA, USA).

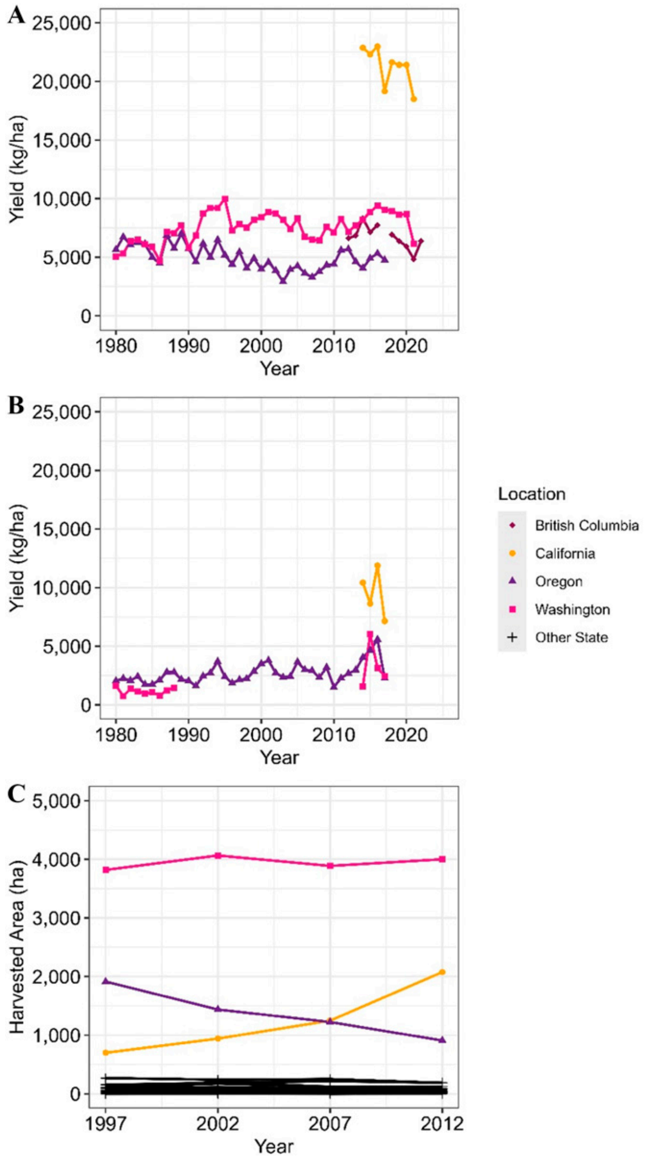

Fig. 1. (**A**) Red raspberry (*Rubus idaeus*) yields in the United States for reporting states and British Columbia, Canada. (**B**) Black raspberry (*Rubus occidentalis*) yields in the United States for reporting states. (**C**) Total harvested raspberry acreage in the United States for reporting states. Based on data from the US Department of Agriculture Economic Research Service (2023), Statistics Canada (2023), and the US Department of Agriculture National Agricultural Statistics Service (2024).

Today, the Corvallis USDA-ARS program (Corvallis, OR, USA) prioritizes blackberry breeding but continues to work on red and black raspberries. The WSU and BCBCDI programs primarily develop elite red raspberry cultivars. The caneberry focus for each program matches regional acreage, with blackberry and black raspberry predominantly grown in Oregon, and red raspberry prevalent in Washington, USA and British Columbia, Canada (Statistics Canada 2023; US Department of Agriculture–Economic Research Service 2023).

Rubus genetic resources are maintained at the USDA-ARS National Clonal Germplasm Repository (NCGR; Corvallis, OR, USA) and were recently described by Bushakra et al. (2020). The NCGR currently maintains more than 2000 *Rubus* accessions from 56 countries. The mission of the NCGR is to acquire and maintain genetic resources, evaluate and characterize them phenotypically and genotypically, and distribute them for research worldwide. Information about these resources is publicly available through the Germplasm Resources Information Network database. The NCGR is

---

Received for publication 12 Mar 2025. Accepted for publication 30 Apr 2025.

This work was funded in part by the US Department of Agriculture (USDA) National Institute of Food and Agriculture (Hatch project no. 7003737), the Northwest Center for Small Fruits Research Center (project no. 2072-22000-046-006-G), and the USDA–Agricultural Research Service (project nos. 2072-21000-060-00D and 2072-22000-046-00D).

Much of the research in caneberries in the Pacific Northwest occurs on the ancestral homelands of indigenous peoples who were forcibly removed through the enactment of various treaties. US land grant universities and colleges that conduct and support this research exist today because of the Morrill Act of 1862, which authorized the sales of expropriated tribal lands to fund the establishment of these institutions.

Mention of tradenames or commercial products in this article is solely for the purpose of providing scientific information and does not reflect recommendation or endorsement by the US Department of Agriculture.

M.A.H. is the corresponding author. E-mail: michael.hardigan@usda.gov.

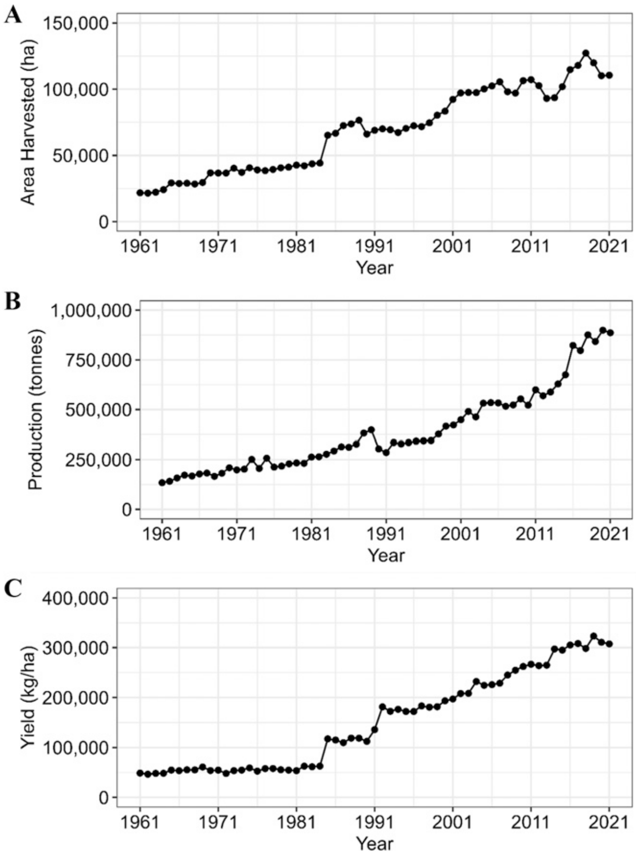

Fig. 2. (**A**) Global red and black raspberry (*Rubus idaeus* and *Rubus occidentalis*) area harvested from 1961 to 2021. (**B**) Global raspberry production from 1961 to 2021. (**C**) Global raspberry yields from 1961 to 2021. Based on data from the Food and Agriculture Organization of the United Nations (n.d.).

vital to caneberry breeders who work closely with the *Rubus* curator and NCGR team on all aspects of acquisition, evaluation, research, and breeding. All NCGR accessions have a unique plant introduction (PI) number that is used to track their identities from distribution to downstream use in published research and breeding.

These programs have produced important public cultivars regionally and globally. Red raspberry 'Meeker' (PI 553384) was released in 1967 from the WSU program and accounts for a small but significant amount of established acreage of red raspberry for the processed market (Moore and Daubeny 1993). Red raspberry 'Tulameen' (PI 618441) out of the AAFC-PARC program set the current standard for fresh-market red raspberry fruit quality in the early 1990s (Daubeny and Anderson 1991; Daubeny and Kempler 2003). Some of the PNW red raspberry cultivars have become important globally and are widely grown, such as 'Willamette' (PI 553362) in Serbia (Leposavić et al. 2013). Red raspberry floricane cultivars for processing continue to dominate the PNW industry, where growers use a combination of public and private cultivars such as 'Cascade Harvest' and 'Cascade Premier' from WSU, 'Chemainus' from the BCBCDI, 'Wakefield' and 'Wakehaven' from Northwest Plant Co., 'Kulshan' from Driscoll's, and other proprietary cultivars (nursery sales data from Northwest Berry Foundation, unpublished information; Moore et al. 2015). Many growers in Oregon, USA, continue to plant historical cultivars such as red raspberry 'Meeker' and black raspberry 'Munger', which is an example of the challenges breeders face in developing and promoting the adoption of new cultivars with high yield, machine-harvested fruit quality, long-term plant health, and resistance to abiotic and biotic stresses.

Table 1. Top 10 countries with the highest production, rounded to nearest whole ton of raspberry in 2021.

Country	Production (t)
Russian Federation	197,700
Mexico	165,677
Serbia	110,589
Poland	103,900
United States	81,150
Spain	48,830
Ukraine	36,290
Portugal	27,950
Bosnia and Herzegovina	16,833
Chile	15,934

Based on data from the Food and Agriculture Organization of the United Nations (n.d.).

Genetic Diversity of Caneberries

Caneberry breeding for commercial production spans the past 200 years (Hall 1990). *Rubus* is an incredibly diverse genus, with 1471 accepted species to date (Plants of the World Online 2023). Of these species, only a few are cultivated for commercial production. Most red raspberry cultivars are diploids ($2n = 2x = 14$) with ancestry that is derived from *R. idaeus* and its close relative *Rubus strigosus*, with occasional hybridization to other diploid *Rubus* subgenus *Idaeobatus* species (Hummer and Hall 2013). Black raspberry cultivars are also mostly diploid ($2n = 2x = 14$) and are predominantly derived from *R. occidentalis*, with occasional use of species hybrids to improve thornlessness, disease resistance, and fruit size.

The taxonomic classification of *Rubus* species is challenging because of apomixis and other nuclear events. Random chromosome doubling, parthenogenesis, meiotic disturbances, or unreduced gametes contribute to ploidy variation (including within species) and species hybridization, making species identification and organization difficult (Hall 1990; Thompson 1997). Most domesticated forms of *Rubus* are monoecious, although there are dioecious species, including several wild progenitors of domesticated forms (Crane and Lawrence 1931). Dioecy is strongly selected against by breeders, resulting in cultivars that are hermaphroditic and readily self-fertilize, which aids drupelet development and fruit set. Numerous cultivars and species are capable of self-fertilization, but some demonstrate inbreeding depression in early generations of progeny, which is a common observation in heterozygous outcrossing species (Daubeny 1971; Fejer and Spangelo 1974). Because of their heterozygous genomes, caneberries are clonally propagated to ensure true-to-type expression of selected plant phenotypes for agricultural production.

The tremendous diversity observed in *Rubus* is both useful and challenging to plant breeders working to improve existing caneberry cultivars and introduce novel traits. Wild accessions and heirloom cultivars can be excellent sources of pest and disease resistance or tolerance. However, eliminating the undesirable characteristics found in these germplasm, including dense prickles, nonerect growth habit, and soft or crumbly fruit, requires years of effort, underscoring the need for genomic breeding tools. Only a handful of cultivars are commonly found in the pedigrees of existing red raspberries. Graham and Jennings (2009) described 'Lloyd George' (PI 643942), 'Pynes Royal', 'Preussen' (PI 553525), 'Cuthbert' (PI 553363), and 'Newburgh' (PI 553369) as being the five parent cultivars that are commonly found in the pedigree of modern cultivars. Hummer and Hall (2013) found that eight cultivars listed in Hedrick's *Small Fruits of New York* (Hedrick 1925) were present in more than 75% of modern cultivars. These eight cultivars were 'Lloyd George', 'Latham' (PI 553564), 'Cuthbert', 'Newman' (PI 553448), 'Viking' (PI 553368), 'Ranere' (PI 553366), 'June' (PI 553561), and 'Herbert'. Although there are some cultivars consistently reported between studies as prominent parents, the differences in the studies are likely the result of a focus on adaptation for specific geographic regions, which appears to be further supported by the assessment conducted by Dale et al. (1993) on the genetic contributions in cultivars by founding clones. Despite their narrow list of founders, phenotypic diversity within PNW red raspberry breeding populations remains high and is supported by continuous introduction of alleles from global germplasm.

Black raspberry development for commercialization has been hampered by numerous undesirable characteristics present in currently available material, such as susceptibility to viral and fungal diseases, small fruit size, and spiny canes (Hummer and Hall 2013; Jennings 1988). Improving such traits has proved difficult because many of the modern black raspberry cultivars have been found to be almost indistinguishable morphologically and genetically (Dossett et al. 2012; Ourecky 1975; Weber 2003). Commercial black raspberry production is concentrated primarily in Oregon in the United States and in South Korea, which has contributed to the slow turnover of cultivars (Graham and Jennings 2009; Kempler and Hall 2013). Black raspberries ‘Munger’ (PI 553740) and ‘Jewel’ (PI 553742) are the main cultivars grown, both of which were released several decades ago (Ourecky and Slate 1973; Weber 2013). In the PNW, production is focused mainly on machine-harvested berries for processing into anthocyanin-rich purées and food products, and breeding efforts are focused correspondingly on improving plant durability and disease resistance or tolerance over fresh-market eating quality.

Historically, the diversity of *Rubus* species has contributed to numerous traits that have become important for the industry, such as the absence of thorns or spines, plant architecture (erect, semierect, trailing), chilling requirement, primocane fruiting habit, fruit size, fruit firmness, and shelf life. Hall and Kempler (2011) described numerous examples of raspberry breeding programs worldwide using noncommercially cultivated species such as *Rubus arcticus*, *R. cockburnianus*, *R. crataegifolius*, *R. odoratus*, *R. spectabilis*, *R. pileatus*, *R. niveus*, *R. innominatus* var. *kuntzeanus*, *R. biflorus*, *R. coreanus*, *R. parviflorus*, *R. parvifolius*, *R. idaeus*, *R. strigosus*, *R. glaucus*, *R. trivalis,* and *R. lasiostylus* for various fruiting qualities, abiotic and biotic stress resistance, and agronomic characteristics. A still wider set of species contribute to the crop hybrid complex that comprises the modern pool of blackberry cultivars. These species have been used to integrate desirable traits into other caneberry types, such as the hybrid cultivars Logan and Boysen, which are derived from combining trailing blackberry species with *R. idaeus* and *R. strigosus*, and supported important niches in the processed-fruit market (Hall et al. 2005). These species as well as underutilized species contained in US gene banks can be used to diversify the current germplasm in PNW and global breeding programs.

Several abiotic and biotic stressors are important in raspberry production, and developing resistant or tolerant cultivars is a significant goal of *Rubus* breeding programs today. Root rot and RBDV resistance are listed consistently as primary objectives for European and North American caneberry breeders (Finn et al. 2008; Weber 2013). In addition, resistance to potato leaf hopper (*Empoasca fabae*) and aphids (*Amphorophora idaei* and *Amphorophora agathonica*), which transmit the mosaic virus complex, are biotic resistance traits of interest. Although “resistance” appears frequently as a breeding objective in publications, it should be noted that “tolerance” can also be beneficial for plant longevity and performance. Pagán and García-Arenal (2018) describe resistance as “the host’s ability to limit pathogen multiplication” and tolerance as “the host’s ability to reduce the effect of infection on its fitness regardless of the level of pathogen multiplication.” The goals of individual plant breeders inform their decisions to pursue incorporating and selecting genetics for resistance or tolerance. Given the availability of germplasm-harboring alleles for resistance and tolerance, both should be incorporated to support a more stable plant pest response and delay the emergence of resistance-breaking pest populations. This may not be possible in the case of pests or pathogens for which breeders have not identified genetic resistance in the germplasm, such as spotted-wing Drosophila (SWD; *Drosophila suzukii*) or *V. dahliae*. As the evolutionary arms race between pathogens and plant hosts continues, it is of little surprise that biotic stress resistance or tolerance remains a central focus of PNW caneberry breeding programs.

Plant Diseases of Caneberries in the PNW

Raspberry producers in the PNW face a variety of biotic stress challenges from pests and pathogens that can severely reduce yield, plant longevity, and marketable fruit quality. Many of these stressors have been an ongoing concern for decades. Chief among them are the plant–parasitic root lesion nematode (*P. penetrans*); the RBDV; the diseases Verticillium wilt (*V. dahliae*), Phytophthora root rot (*Phytophthora rubi*), and gray mold (*Botrytis cinerea*); and the insects SWD (*D. suzukii*), the American large raspberry aphid (*A. agathonica*), and the rose stem girdler (*Agrilus cuprescens*) (Gigot et al. 2013; Martin 1998; Weiland et al. 2018). This review focuses on these diseases and pests. Other known and emerging diseases and pests have been discussed in detail by Crandall (1995), Finn and Hancock (2008), Hall et al. (2009), and Dolan et al. (2018).

Root lesion nematode (P. penetrans). Root lesion nematodes (*Pratylenchus* spp.) are globally widespread plant parasites that affect many crops. In a 2012 survey (Jones et al. 2013), these nematodes were voted as the third most economically important group of nematodes. They are polyphagous, migratory endoparasites found near and in roots of plants (Fig. 3A and B). As their name suggests, feeding on roots creates lesions and necrotic areas, resulting in reduced root growth and even plant death. Severe feeding affects aboveground biomass, reducing growth and crop yield (Fig. 3C and D). Their migratory

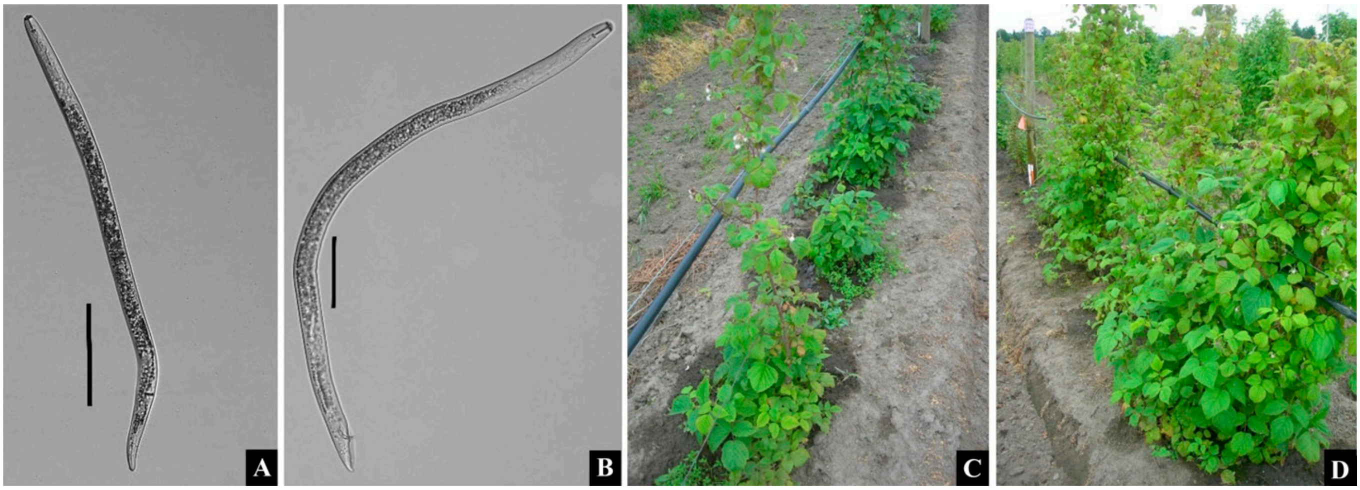

Fig. 3. (**A**) *Pratylenchus penetrans* female at a 100-µm scale. (**B**) *Pratylenchus penetrans* male at a 50-µm scale. (**C**) ‘Willamette’ red raspberry plants in unfumigated, *P. penetrans*–infested soil. (**D**) ‘Willamette’ red raspberry plants in soil fumigated for *P. penetrans.* Photos courtesy of Lester Núñez-Rodríguez, Oregon State University, and Inga Zasada, US Department of Agriculture–Agricultural Research Service.

nature and lack of obvious feeding patterns make them a challenging pathogen to investigate (Castillo and Volvas 2007; Jones and Fosu-Nyarko 2014).

Pratylenchus penetrans parasitizes more than 400 plant species, including red raspberry (Castillo and Volvas 2007; Rudolph and DeVetter 2015; Zasada et al. 2015). This nematode is of special importance for red raspberry in the PNW because of the limited environmental range suitable for red raspberry production (Rudolph and DeVetter 2015) and because raspberry-grower profit margins are narrow (Walters et al. 2017), making economical and sustainable control methods critical for growers. This pest also affects red raspberry production significantly in Scotland and other parts of Europe (Hall et al. 2009).

Historically, fenamiphos and methyl bromide were important nematicides used in the United States to control this pest. As environmental standards and policies have tightened, approved fumigants have become fewer and more difficult to use, reducing grower access to effective chemical treatments for nematodes (US Environmental Protection Agency 2008; Zasada et al. 2010). The raspberry industry in the PNW relies heavily on soil fumigation and primarily uses 1,3-dichlorpropene for preplant fumigation to reduce nematode densities, primarily focused on *P. penetrans* (Zasada et al. 2010). Investigations into nonchemical strategies to manage *P. penetrans* have included brassicaceous seed meal, compost, mulch, root removal, solarization, cover crops, and crop rotation (DeVetter et al. 2018; Forge and Kempler 2009; Forge et al. 2012, 2014, 2016; Gigot et al. 2013; Pinkerton et al. 2000, 2009; Rudolph et al. 2017, 2018, 2019b; Trudgill and Brown 1992; Vrain et al. 1996; Walters et al. 2017; Zasada et al. 2009). Most of these strategies were not found to be comparably effective compared with soil fumigation, or were uneconomical for the grower, leaving preplant soil fumigation as the primary industry method for nematode management. Available fumigant treatments can reduce nematode densities, but the nematode is never eliminated from a field.

Raspberry bushy dwarf virus. RBDV is a pollen-borne viral disease that is characterized by poor drupelet set and crumbly fruit in some infected plants, and is accentuated by coinfections with *Raspberry leaf mottle virus* (RLMV) and *Raspberry latent virus* (RpLV) (Martin et al. 2013; Quito-Avila et al. 2014). RBDV resistance is a major objective in raspberry breeding programs. Although commercial cultivars are often symptomless when infected only with RBDV, the namesake dwarf phenotype arises when coinfections with *Black raspberry necrosis virus* (BRNV) occur (Jones 1979). Fruit from infected plants is susceptible to crumbling resulting from weak drupelet set or drupelet abortion (Murant et al. 1974). As a result, fruit may be rejected from the high-value individual quick-frozen market by processors, forcing growers to sell their fruit into lower grade juice, jam, or crumbled fruit markets (Washington Red Raspberry Commission, unpublished information). Losses from poor fruit set caused by RBDV are estimated to be as high as \$2470/ha per year (Moore and Martin 2008).

RBDV was originally classified among the tripartite ilarviruses of the family Bromoviridae before being classified into a new genus *Idaeovirus* within Bromoviridae and was most recently placed into the family Mayoviridae because of its genomic properties (Martin and Keller 2021; Ziegler et al. 1992, 1993). Isometric virions are ~33 nm in diameter and are composed of a single-stranded RNA bipartite genome with RNA-1, RNA-2, and RNA-3 (Barnett and Murant 1970; Mayo et al. 1991; Natsuaki et al. 1991; Ziegler et al. 1992). RNA-1 is 5449 nucleotides and RNA-2 is 2231 nucleotides; both are genomic RNA. RNA-3 is 946 nucleotides and has been classified as a subgenomic monocistronic coat protein messenger RNA derived from RNA-2. To date, RBDV remains the only officially accepted species in the *Idaeovirus* genus (International Committee on Taxonomy of Viruses 2011). While predominantly a concern in Rubus, plants in the families Amaranthaceae, Chenopodiaceae, Cucurbitaceae, Leguminosae, and Solanaceae were also hosts after manual sap inoculation, but the virus did not readily spread from Rubus to these plants (Barnett and Murant 1970). RBDV was graft transmissible in other Rosaceae species such as quince (*Cydonia oblonga*), the hybrid *Pyronia veitchii*, and alpine strawberry (*Fragaria vesca*) (Credi et al. 1986; Jones et al. 1982). The first report of a natural infection of RBDV outside of raspberry was in grape (*Vitis vinifera*) in Slovenia and later also in Serbia, but has since been reported in sweet cherry (*Prunus avium*) in Turkey (Çağlayan et al. 2023; Jevremović and Paunović 2011; Mavrič et al. 2003; Mavrič Pleško et al. 2009).

A significant challenge in breeding for RBDV resistance is the nature of transmission. The pollen-borne virus is transmitted horizontally and vertically, resulting in infections of nearby plants and resulting seed (Barnett and Murant 1970; Cadman 1965; Murant et al. 1974). Because raspberries rely on insect pollinators, this appears to contribute to horizontal transmission, but there are no known insect vectors (Bulger et al. 1990; Murant et al. 1974). A needle nematode, *Longidorus juvenilis*, was reported to be positive for RBDV; the vector status of this nematode is still being investigated (Mavrič Pleško et al. 2009). Insecticides do not appear to reduce viral spread. Current management recommendations are to cultivate virus-free plants away from wild *Rubus* stands such as thimbleberry (*R. parviflorus*), which can harbor the virus. Growing virus-infected plants appeared to contribute to viral spread more than field proximity to wild stands (Špak and Kubelková 2000). However, eliminating RBDV from infected plants for continued use as parents and selections in breeding is difficult and time-consuming, even with the aid of tissue culture and thermotherapy (Chambers 1961; Lankes 1995; Mathew et al. 2021; Theiler-Hedtrich and Baumann 1989). For these reasons, RBDV is a major challenge not only in grower fields, but also for nursery propagation and maintenance of virus-free breeding populations.

Phytophthora root rot (P. rubi). *Phytophthora rubi* [Wilcox and Duncan (Man in't Veld 2007)] is an economically significant soilborne pathogen of red raspberry commonly found in Washington, USA; British Columbia, Canada; and the northeastern United States (Gigot et al. 2013; Sapkota et al. 2022; Stewart et al. 2014; Weiland et al. 2018; Wilcox 1989). Black raspberries may also be infected but are generally much less susceptible (Fiola and Swartz 1994; Funt 2013; Wilcox and Cooke 2017). In addition to *P. rubi*, other *Phytophthora* species, such as *P. cactorum* and *P. megasperma*, may be important locally or regionally (Montgomerie and Kennedy 1980; Weiland et al. 2024; Wilcox 1989). *Phytophthora rubi* often co-occurs with other soilborne pathogens, including *P. penetrans*, *V. dahliae*, and various other *Fusarium*, *Cylindrocarpon*, *Rhizoctonia*, and *Pythium* species (Gigot et al. 2013; Weiland et al. 2018). Together, these pathogens are suspected of forming a soilborne disease complex that contributes to an overall decline in raspberry health, productivity, and field longevity (Weiland et al. 2018). However, *P. rubi* appears to be among the most damaging of the soilborne pathogens, and fields where *P. rubi* occurred were more than twice as likely to have severe root rot symptoms than fields where it did not occur.

Phytophthora species are not true fungi, but are more closely related to brown algae, and are properly classified as oomycetes (water molds). Oomycetes produce motile spores (zoospores) in response to high soil moisture. Zoospores are attracted to root exudates, and swim to fine roots where they initiate infection. Excessive irrigation, precipitation, or poor drainage can exacerbate infection and lead to significant plant loss (Duncan and Kennedy 1989; Wilcox and Cooke 2017). *Phytophthora rubi* zoospores are likely produced in late spring and summer, when field soils are warm, near 21 °C (Graham et al. 2021). Most *Phytophthora* species also produce thick-walled survival spores (either chlamydospores or oospores), which can survive for years in the soil. Combined, these characteristics can cause root rot to develop very rapidly when conditions are optimal, and make the pathogen extremely difficult to control in infested fields.

Once infection has occurred, *P. rubi* rots the fine roots, leaving larger structural roots behind. Lesions may develop on large roots and extend above the soil line into the lower cane, which may shrivel and turn reddish brown to purple or black (Stewart et al. 2014; Weiland et al. 2018; Wilcox and Cooke 2017). Scraping away the bark reveals water-soaked, reddish brown lesions with a distinct margin between recently killed and healthy tissues (Fig. 4A). Injured roots become increasingly unable to transport water and nutrients, leading to aboveground symptoms of stunting, wilting, leaf chlorosis or reddening, and cane death (Fig. 4A and B). These symptoms may occur on only one or two canes, or may affect the entire plant. Severe infections can cause up to 100% plant mortality

Fig. 4. (**A**) Scraped red raspberry (*Rubus idaeus*) root revealing the water-soaked, reddish lesion typical of *Phytophthora rubi* infection. (**B**) Whole-plant symptoms of *P. rubi* infection in red raspberry. Photos courtesy of Jerry Weiland, US Department of Agriculture–Agricultural Research Service.

in grower fields (Gigot et al. 2013; Weiland et al. 2018).

In the PNW, a combination of preplant soil fumigation, raised beds, resistant cultivars, and fungicides are used to manage *P. rubi*. Several fungicides are available and effective, including mefenoxam, phosphorous acid, and oxathiapiprolin (Heiberg 1995, 1999; Sapkota et al. 2023a, 2023b; Weiland et al. 2024; Wilcox et al. 1999). Amendments such as gypsum have been investigated and have shown promising results as part of a successful integrated pest management plan in conjunction with raised beds, resistant cultivars, solarization, and chemical controls (Maloney et al. 1993, 2005; McGregor and Franz 2002; Pinkerton et al. 2009). Biological controls have also been investigated in vitro but have not yet been examined under field conditions (Toussaint et al. 1997; Valois et al. 1996).

Verticillium wilt (V. dahliae). Although *P. rubi* is the most destructive root pathogen of red raspberry, *V. dahliae* is the most damaging root and vascular pathogen of black raspberry (Mercier and Kong 2017). Unlike *P. rubi*, *V. dahliae* is a true fungus. It can survive in field soil for decades as hard, microscopic structures called microsclerotia. Microsclerotia germinate in response to root exudates and infect the fine roots of susceptible plant hosts. Once infection has occurred, the pathogen plugs and kills the water-conducting tissues (xylem), leading to wilting and cane death (Fig. 5). Unlike *Phytophthora* species, *V. dahliae* does not cause root decay, thus the fine root system may still be intact on recently killed plants. Infected canes may be discolored purple to black and are very similar in appearance to canes killed by *P. rubi*. Therefore, plant samples should be sent to a diagnostic laboratory to confirm which pathogen is present, because many fungicides used to manage *P. rubi* are ineffective against *V. dahliae*.

Although red raspberry is not as susceptible to *V. dahliae* as black raspberry, severe infection is observed occasionally, especially when caneberries are grown in fields that were cropped previously with potato (*Solanum tuberosum*) or mint (*Mentha* spp.) (Weiland et al. 2018). Both mint and potato are highly susceptible to *V. dahliae*, and cropping with either of these plants can cause soil populations of the pathogen to build up to extremely damaging levels, resulting in major damage on caneberries grown in the field afterward.

Verticillium wilt is extremely difficult to manage once a field becomes infested. In woody crops, the disease is most commonly managed by either not planting susceptible crop species into fields where the pathogen is present or by preplant fumigation under tarp (Mercier and Kong 2017). This is a challenge in Oregon, where black raspberry is commonly planted in fields that previously contained other host crops such as potato. Unfortunately, there are no known fungicides that are effective against this disease. Solarization can reduce soil populations of the pathogen (Pinkerton et al. 2000), but the effect is inconsistent and does not penetrate deeply enough into the soil profile to provide effective, long-lasting disease control in northern locations. Host resistance has not been well explored in black raspberry cultivars, although hybrids containing red raspberry parentage were more tolerant of Verticillium wilt than those containing only black raspberry parentage (Fiola and Swartz 1994). Similarly, only one or two of 17 black raspberry accessions had low symptom severity after inoculation in a greenhouse screening assay, although this effect was intermittent and severe disease was occasionally seen on all 17 genotypes (Weiland JE, unpublished data).

Gray mold (B. cinerea). *Botrytis cinerea* is a necrotrophic, haploid, ascomycete fungus that affects more than 1400 plant species worldwide (Alfonso et al. 2000; Fillinger 2016; Garfinkel et al. 2019; Ma and Michailides 2005; Staats et al. 2005; Williamson et al. 2007). *Botrytis cinerea* is the causal agent of cane blights, rots, and gray mold, a globally destructive disease that causes significant yield loss of red raspberry in the field and postharvest (Elad et al. 2004; Leroux 2007). The regional climate in the PNW contributes to high disease pressure from *Botrytis* spp. on red raspberry. *Botrytis* spp. can infect any foliar part of the plant, particularly leaves, buds, flowers, or fruit at a variety of developmental stages (Fig. 6) (Williamson et al. 2007). Infection of raspberry flowers and berries reduced yield and berry quality directly (Dashwood and Fox 1988; Kozhar and Peever 2018). The global annual cost to control *B. cinerea* exceeds $1 billion/year and management relies heavily on the use of synthetic fungicides (Leroux 2007; Yin et al. 2012).

Botrytis cinerea is a high-risk fungal pathogen for the development of fungicide resistance as a result of its rapid life cycle, genetic diversity, and high fecundity (Atwell et al. 2015; Hahn 2014). Resistance to Fungicide Resistance Action Committee (FRAC) classes, including demethylation inhibitors, succinate dehydrogenase inhibitors, and quinone outside inhibitors has been reported worldwide (Hahn 2014; Zhang et al. 2016) and is a serious limitation for effective disease control. In the PNW, the primary management strategy for gray mold has been the use of fungicides with single-site modes of action (Hahn 2014). Growers often alternate fungicides with different FRAC codes, determined by their modes of action, to slow the development of resistance (Konstantinou et al. 2015; Polat et al. 2018; Zhang et al. 2016).

Further investigations have revealed there are genetic differences in *B. cinerea* populations with regard to fungicide sensitivities (Fournier et al. 2002; Konstantinou et al. 2015; Leroux et al. 2002; Martinez et al. 2005; Martínez et al. 2008). Differences in fungicide resistance profiles could be related to high levels of genetic diversity and restricted gene flow among the different cryptic groups of *B. cinerea* (Fournier et al. 2002, 2005; Giraud et al. 1997; Leroux et al. 2002; Martinez et al. 2003; Martínez et al. 2008; Walker et al. 2011). Fournier and Giraud (2008) demonstrated high *Botrytis* spp. genetic diversity within fields. Hu et al. (2018) showed a high diversity between isolates from the same location, and even on the same host plant, with multiple haplotypes exhibiting different fungicide-resistant profiles existing on the same plant

Fig. 5. (**A**) Red raspberry (*Rubus idaeus*) with symptoms of *Verticillium dahliae* infection, (**B**) Black raspberry (*Rubus occidentalis*) with symptoms of *V. dahliae* infection. Photos courtesy of Jerry Weiland, US Department of Agriculture–Agricultural Research Service.

Fig. 6. (**A**) Ripe red raspberry (*Rubus idaeus*) fruit during harvest, infected with *Botrytis cinerea* conidia. (**B**) *Botrytis cinerea* producing millions of spores on red raspberry cane lesion. Photos courtesy of Jeff DeLong, US Department of Agriculture–Agricultural Research Service.

tissue. The high genetic diversity of these pathogens and lack of clear genetic resistance in commercially elite germplasm make it a challenge to address by breeding efforts.

Insect Pests of Caneberries in the PNW

Spotted-wing Drosophila (D. suzukii). Originating in east Asia, SWD (syn. Asian vinegar fly; *D. suzukii*) has become one of the most important insect biotic stresses for small fruits and stone fruits such as blueberry, caneberries, strawberry, and cherry within the past two decades (Lee et al. 2011). It was introduced to the continental United States in California in 2008, and by 2015, was present in most states (Asplen et al. 2015). Compared with other fruit, red raspberry is a preferred host for SWD (Bellamy et al. 2013; Burrack et al. 2013).

This fly has a serrated ovipositor that allows it to penetrate the fruit skin and lay eggs within ripening fruit (Fig. 7A). The developing larvae feed on the fruit tissue, inflicting heavy damage. The infested fruit is subject to rejection by fruit packers, sellers, and importers because of the presence of SWD, infections from other pathogens resulting from SWD damage, and violations of maximum residue limits from pesticide applications (Goodhue et al. 2011). In California, crop damage from SWD can lead to temporary price increases for growers, but overall represents significant revenue reductions (Goodhue et al. 2011).

Since its introduction, there has been heavy reliance on insecticides to manage SWD, but in recent years there has been emerging research demonstrating the use of biological control agents (e.g., parasitoid wasps, insect and avian predators, entomopathogenic nematodes), nonhazardous sugar substitutes (e.g., erythritol), and physical barriers and deterrents (e.g., exclusion netting, plastic mulch) for management (Carroll et al. 2023; Choi et al. 2017; Lee et al. 2019; McIntosh et al. 2023; Sampson et al. 2017; Stockton et al. 2020). Since 2022, releases of the imported parasitoid *Ganaspis kimorum* have been made throughout the United States, and another parasitoid originally from Asia, *Leptopilina japonica*, has established on its own throughout North America (Gariepy et al. 2024). The impacts of these parasitoids on SWD populations are being monitored.

American large raspberry aphid (A. agathonica). The large raspberry aphid (syn. raspberry aphid, common raspberry aphid) is a significant concern for red raspberry production in North America and Europe. The species differ between the two locations. The American large raspberry aphid is *A. agathonica* (Fig. 7B), whereas the European large raspberry aphid is *A. idaei*.

Feeding on raspberry plants by the American large raspberry aphid can result in leaf curl, which on its own is not detrimental to the plant (Funt 2013). The detrimental effect is the aphid's role as a vector for many of the viruses that contribute to the raspberry mosaic virus complex and the raspberry crumbly fruit complex. The raspberry mosaic virus complex includes BRNV, RLMV, and *Rubus yellow net virus* (RYNV) (Martin et al. 2013). The raspberry crumbly fruit complex is comprised of RBDV, RLMV, RYNV, and RpLV (Martin et al. 2013). Of all these viruses, RBDV is the only one that is not transmitted by aphids (refer to earlier section). To add to this complexity, each of these viruses are transmitted in variable manners, with BRNV transmitted nonpersistently, RYNV and RLMV likely transmitted semipersistently, and RpLV transmitted persistently (Cadman 1954; Halgren et al. 2007; Jones et al. 2002; Quito-Avila et al. 2012).

Options for aphid management include biocontrols (e.g., parasitic wasps), cultural controls (e.g., removal of plant debris), chemical controls (e.g., imidacloprid), and plant genetic resistance. No genes have been identified that confer resistance to these viruses, and research has therefore focused on improving resistance to the insects that transmit virus.

Rose stem girdler (A. cuprescens). Since 2022, the rose stem girdler has been found from the southern Willamette Valley of Oregon, USA, to the Canadian border of western Washington, USA (O'Dea 2024). Introduced from Europe, it was first reported in the eastern United States as early as 1913.

The insect is a metallic-colored beetle that lays its eggs on the canes of various *Rubus* species and rose plants (Fig. 7C). The hatched larvae tunnel and feed inside the cane that girdles the canes. Girdling can cause galling in first-year canes, can increase cane snapping and breakage significantly, and can reduce fruit production in second-year canes. Heavy infestation for 2 to 3 years will kill plants. The larvae overwinter inside the canes and emerge as adults from late May to early June after accumulating ∼900 h at more than 55 °F (O'Dea and Hill 2022).

Effective monitoring with traps for the rose stem girdler is still in need of development. Currently, growers are recommended to use insecticides for 3 weeks after pest emergence,

Fig. 7. (**A**) *Drosophila suzukii* on ripe red raspberry (*Rubus idaeus*) fruit. (**B**) Colony of *Amphorophora agathonica* in various life stages feeding on a black raspberry (*Rubus occidentalis*) seedling. (**C**) *Agrilus cuprescens* on a blackberry leaf. Photos courtesy of Savannah Phipps, Oregon State University; Victoria Skillman, US Department of Agriculture–Agricultural Research Service; and Justin O'Dea, Washington State University.

and to prune canes with damage. Pruned canes need to be removed or destroyed to kill the overwintering larvae. A parasitoid that attacks the larval stage, *Baryscapus rugglesi*, has been found regularly in the PNW (O'Dea et al. 2023). Because this parasitoid is already naturally occurring, a greater understanding of conservation practices to enhance its effectiveness is needed.

Current Understanding of Disease Resistance Genetics

For the diseases and pests discussed earlier, management has been ongoing for decades, primarily with chemical methods. Understanding the impacts that certain pesticides have on environmental and human health has improved in the 21st century, reducing the availability of previously approved chemicals. Although innovative alternates to chemical control show some promise, many are ineffective or not economically feasible. In many cases, genetic resistance is the most sustainable and economical form of management despite the occasional emergence of new resistance-breaking pests or pathogens. Sources of genetic resistance to several pests and pathogens have been identified in red raspberry, although our knowledge remains limited for many of these biotic stresses.

Genetics of root lesion nematode resistance. Bristow et al. (1980) evaluated the reaction of 18 red raspberry cultivars to *P. penetrans* and found that some cultivars showed heavy infestations by *P. penetrans*, but with no significant impact on biomass fresh weight compared with the controls. This suggested that the raspberries under investigation possessed varying degrees of tolerance to *P. penetrans*; however, the authors speculated that the method used may not have elicited a significant response from the plants. Vrain and Daubeny (1986) performed a similar experiment with 21 red raspberry genotypes, including 10 from the experiment by Bristow et al. (1980) and four related *Rubus* cultivars. Some cultivars demonstrated tolerance, and some demonstrated resistance based on the number of nematodes present and effects on plant growth and development, perhaps indicating that tolerance may be sustained for some time before a plant shows symptoms of *P. penetrans* parasitism. More recently, Zasada and Moore (2014) evaluated the reaction of a panel of *Rubus* species to *P. penetrans* in a greenhouse trial, including some of those from the Vrain and Daubeny (1986). The host status of *R. crataegifolius* 'Jokgal' was inconclusive in this trial, although Vrain and Daubeny (1986) previously found 'Jokgal' to support low densities of *P. penetrans*. Zasada and Moore (2014) observed that two black raspberry species, *R. niveus* and *Rubus leucodermis*, were poor hosts for *P. penetrans* across years and that they may be useful in breeding programs. However, raspberry 'Tulameen' (PI 618441) (Daubeny and Anderson 1991), which has *R. niveus* in its pedigree, did not support lower *P. penetrans* densities consistently compared with the industry standard 'Meeker'.

Current information on the host status of various clones and insights into the genetics of *P. penetrans* resistance suggest that *P. penetrans* resistance is quantitative and influenced by genetic background. Vrain et al. (1994) further investigated the mode of inheritance for *P. penetrans* resistance using a half-diallel analysis with crosses between two resistant and two susceptible genotypes. Resistance of red raspberry to *P. penetrans* was determined to be a quantitative trait, as no bimodal distributions indicative of a qualitative trait were observed for the recorded traits. A limitation of that study was its small sample size. Larger family size may reduce variability and allow determination of the resistance inheritance mode. To date, no published studies have evaluated and characterized *P. penetrans* resistance using genomic or quantitative genetic approaches.

Genetics of RBDV resistance. A single resistance gene to RBDV known as *Bu* was identified in the early 1980s (Jones et al. 1982; Murant et al. 1982). This is a dominant gene that appears to confer complete immunity to Scottish or common RBDV isolates (RBDV-S). Resistant cultivars possessing *Bu* are heterozygous. Cultivars homozygous for *Bu* were not identified, suggesting that the homozygous state may be deleterious to plant health or is in linkage with other deleterious alleles (Stephens et al. 2016). Since the discovery of the *Bu* gene, there have been intensive efforts to incorporate this gene while maintaining other desirable traits. Stephens et al. (2016) located potential markers for use in marker-assisted selection (MAS), as did Ward et al. (2012). However, marker accuracy was dependent on pedigree, and additional work is needed to determine marker usefulness for breeding. Genetic engineering has also been explored as an avenue for RBDV resistance. Red raspberry 'Meeker' was transformed successfully with the coat and movement protein genes of RBDV using *Agrobacterium*-mediated transformation to confer resistance to the common RBDV isolates (Martin and Mathews 2001; Martin et al. 2001). However, public wariness and governmental regulations of transgenic plants have impeded the advancement of these plants for cultivation or use as parents for breeding resistant progeny.

After the identification of *Bu*, resistance-breaking isolates were discovered in 1981 in the United Kingdom at about the same time that seed from the former Union of Soviet Socialist Republics was introduced to the area (Barbara et al. 1984; Knight and Barbara 1981; Murant et al. 1982). Identifying additional sources of resistance became very important. Previous studies indicated the presence of additional resistance genes that were never fully identified, but which appeared to provide quantitative resistance to the resistance-breaking isolate when *Bu* was also present (Jennings and Jones 1989; Jones et al. 1982). Although resistance-breaking isolates have been observed in the United Kingdom and other European countries, the first report in the United States came from Washington in 2014 (Lanning 2014; Lanning et al. 2016). A viral survey would be of great benefit to researchers and breeders as there have not been any further reports of this strain in the United States.

Genetics of Phytophthora root rot resistance. Identifying and understanding Phytophthora root rot has been a significant goal of breeding programs in the PNW since the 1970s, and in the United Kingdom since the 1980s (Barritt et al. 1979, 1981; Knight et al. 1989). Barritt et al. (1979) screened germplasm for resistance or susceptibility to Phytophthora root rot and determined high heritability estimates for resistance, concluding that resistance was additive, and rapid genetic gain was achievable. Knight and Fernández-Fernández (2008) evaluated the nature of resistance in a half-diallel analysis and suggested that resistance was an additive, quantitative trait. Similar results were obtained by Nestby and Heiberg (1995); however, they found that nonadditive gene action occurred as well.

As molecular techniques have advanced, our understanding of the underlying genetic mechanisms and modes of inheritance for Phytophthora root rot resistance has improved and reinforced some of the conclusions of past studies. Like Nestby and Heiberg (1995), Pattison et al. (2007) demonstrated multiple gene actions. Depending on the trait being measured (petiole lesion incidence and plant disease index), additive or dominance effects may have accounted for a significant proportion of the variance. Their results suggested other gene effects contributed to recorded phenotypes alongside additive and/or dominance effects, and Pattison et al. (2007) proposed that qualitative or quantitative measures could be used to evaluate and improve resistance. The application of molecular markers for selecting resistant genotypes was demonstrated by Weber et al. (2008), who found that a sequence characterized amplified region marker and a cleaved amplified polymorphic sequence marker were 62% and 56% accurate, respectively, in selecting a resistant individual. Use of both markers allowed for the retention of 85% of resistant individuals. Additional quantitative trait loci (QTLs) associated with Phytophthora root rot resistance allowed for further investigation into potential mechanisms of resistance, such as the involvement of auxin or germin-like protein in the initiation of new axial growth as a defense response. These QTLs can support the development of predictive molecular marker assays to increase selection efficiency for resistant raspberry progeny using MAS (Graham et al. 2011; Pattison et al. 2007).

Several available red raspberry cultivars have desirable levels of Phytophthora root rot resistance, including 'Latham' and 'Asker'. In addition, wild, uncultivated species have been examined as novel sources of genetic resistance for root rot (Barritt et al. 1979; Røen et al. 2012). Several of these species possess desirable resistance levels, such as *R. spectabilis*, as well as *R. coreanus*, *R. inominatus*, *R. niveus*, *R. lasiostylus*, and *R. strigosus* (Kempler et al. 2012; Knight 1991). Breeding efforts by the WSU raspberry breeding program for improving red raspberry resistance to Phytophthora root rot has produced several notable red raspberry cultivars from the ‘Cascade’ series with moderate to high levels of resistance, including ‘Cascade Delight’, ‘Cascade Harvest’, ‘Cascade Bounty’, and ‘Cascade Dawn’ (Moore 2004, 2006; Moore and Finn 2007; Moore et al. 2015).

Genetics of Verticillium wilt resistance. Despite the importance of Verticillium wilt in black raspberry production, there are few publications elucidating resistance or sources of resistance. No resistance to Verticillium wilt has been reported for released black raspberry cultivars (Fiola and Swartz 1994; Zeller 1936). Resistance in red raspberry and blackberry has been established. Red raspberry cultivars such as ‘Antwerp’, ‘Cayuga’, ‘Cuthbert’, ‘Marlboro’, ‘Ohta’, ‘Owasco’, ‘Seneca’, ‘Superlative’, and ‘Syracuse’ can potentially serve as sources of resistance for black raspberry breeding (Darrow 1937). However, cultivars resistant to one strain of *V. dahliae* may not be resistant to others, as noted by Zeller (1936). Resistance and tolerance have been further demonstrated in Asiatic species of red raspberry (Zeller 1936). Native PNW species, *R. spectabilis* and *R. parviflorus*, had minimal to no symptoms of infection and serve as additional sources of resistance. Other regional species such as *R. leucodermis* are long-lived in the face of infection, but with significant yield losses.

Early breeding efforts indicated that the mechanisms of resistance may be quantitative. Backcrossing to red raspberry has not resulted in distinct segregating phenotypes. In addition, progeny in subsequent generations show weak or no resistance, suggesting that numerous small-effect genes may be at play (Keep 1976, 1989). A partial diallel analysis also indicated additive gene action and tolerance rather than resistance (Fiola and Swartz 1994). *Verticillium dahliae* was isolated from resistant cultivars, indicating these plants remained economically productive under infection (Fiola and Swartz 1994). More recently, an RNA sequencing study was performed to identify candidate genes involved in *V. dahliae* infection in black raspberry (Bushakra et al. 2016). Several transcripts were identified as homologs to the *Ve1* resistance gene in tomato, but were not detected among the differentially expressed genes (DEGs) characterized in the study. Other general pest and pathogen response genes were observed among the DEGs. The identification of these genes in response to *V. dahliae* infection presents the opportunity to understand tolerance in black raspberry more fully.

Genetics of B. cinerea *resistance.* The earliest publications from breeding programs detailed the struggle to develop cultivars with *Botrytis* resistance. One of the primary complications is that the same causal organism causes two diseases: cane *Botrytis* and gray mold (syn. fruit *Botrytis*). Cane *Botrytis* appears to be a significant contributor to gray mold development in fruit (Jennings and Brydon 1989). Knight (1980a) also found a positive correlation between cane *Botrytis* and gray mold incidence. Jennings and Carmichael (1975) recommended selecting individuals resistant to cane *Botrytis* and gray mold to reduce inoculum. In contrast, other researchers determined there was no strong correlation between cane *Botrytis* and gray mold development and stated that prior reports of significant correlations were the result of a few strong correlations in evaluated cultivars (Daubeny and Pepin 1981; Knight 1980b).

Decades of research by breeding programs in British Columbia, Scotland, and England indicate that cane *Botrytis* resistance is complex and is likely conferred by a combination of additive, minor genes and few major genes (Daubeny 1987; Jennings 1983; Jennings and Brydon 1989). Gene *H*, which is responsible for cane pubescence, also appeared to be associated significantly with cane *Botrytis* resistance (Graham et al. 2006), although not strongly (Knight 1980a). Whether this association was a result of linkage with resistance genes or physiological differences that deterred infection is unknown (Graham et al. 2006). Resistance not associated with gene *H* has been noted to be present in the Asiatic species *R. pileatus*, *R. crataegifolius*, *R. coreanus*, and *Rubus mesogaeus* and the North American species *R. occidentalis* and *R. strigosus* (Jennings 1983; Jennings and Brydon 1989; Jennings and Williamson 1982; Keep et al. 1977; Knight 1980a, 1980b). It is believed that red raspberry ‘Chief’ (PI 553508) inherited this resistance from the *R. strigosus* in its pedigree (Daubeny 1987).

Most of the published studies in postharvest fruit rot resistance date back at least 45 years. Resistance has been observed in *R. occidentalis*, *R. crataegifolius*, and *Rubus phoenicolasisus* (Kichina 1976; Knight 1980a, 1980b). Red raspberry ‘Matsqui’ (PI 553391) and ‘Cuthbert’ have repeatedly demonstrated low gray mold incidence in fruit rot testing procedures (Barritt 1971; Daubeny and Pepin 1969, 1974). Red raspberries ‘Carnival’ (PI 553481), ‘Meeker’, ‘Glen Isla’ (PI 553510), ‘Nootka’, and ‘Ottawa’ have also been reported to have low gray mold incidence (Barritt 1971; Daubeny and Pepin 1969, 1974). Combined, it appears that there is tolerance primarily occurring in the cultivars reported to have low disease incidence. Furthermore, there appears to be correlations in berry color and other characteristics to resistance, as Harshman et al. (2014) found purple and black raspberries resisted rot the longest. Resistant raspberries had the highest phenolics and anthocyanins and the lowest ethylene evolution rates, which may be contributing to delayed disease development. The researchers suggested that breeding for low ethylene production of berries may protect against rot.

Current Understanding of Insect Pest Resistance Genetics

Genetics of SWD resistance. Host plant resistance is also critical in integrated pest management, although few studies related to SWD have occurred in red raspberry. Strong resistance against SWD has not been observed, but some cultivars are more susceptible to SWD than others (Burrack et al. 2013; Lee et al. 2011; Wöhner et al. 2021). Lee et al. (2011) found no difference in susceptibility to SWD for six cultivars (Table 2). Burrack et al. (2013) also evaluated several berry crops, including nine red raspberry cultivars (Table 2), against SWD and detected variable infestation rates but no resistance among cultivars. However, there was a need to validate the apparent reduced preference among cultivars, which had lower infestation rates (Burrack et al. 2013). Wöhner et al. (2021) evaluated 37 floricane and 23 primocane fruiting red raspberry cultivars and confirmed previous reports of varying levels of susceptibility and an absence of strong resistance to SWD. Of the 60 cultivars tested, only ‘Dorman Red’ (PI 553425), a Mississippian floricane fruiting type (Overcash 1972), and ‘Pokusa’, a Polish primocane fruiting type, were classified as tolerant. Infestation appeared to be strongly correlated to berry firmness, but was not correlated with Brix and acidity. This finding contrasts with previous reports of a positive correlation between Brix and SWD development, and a lack of correlation with pH (Lee et al. 2011). Many other cultivars have not been evaluated, and assessing common PNW raspberry cultivars for susceptibility to SWD would be useful.

Genetics of American large raspberry aphid resistance. Genetic resistance to *A. agathonica* has been studied since the 1920s to mitigate the spread of the raspberry mosaic virus complex (Rankin 1927; Rankin and Hockey 1922). Research has indicated separate resistance genes to *A. idaei* and *A. agathonica*, which were thought to be the same species before the discovery of these genes (Hill 1956).

To date, few known resistance genes to *A. agathonica* have been identified in raspberry. Resistance genes Ag_1, Ag_2, Ag_3, Ag_4, and Ag_5, and an undesignated resistance gene (syn. Ag_6) have been discovered in plants from the northeastern United States or southeastern Canada (Daubeny 1966; Daubeny and Stary 1982; Dossett and Finn 2010). In contrast, 13 resistance genes to *A. idaei* are known in Europe (A_1–A_{10}, A_{K4a}, A_{L518}, and A_{cor}) (Fernández-Fernández et al. 2013; Knight et al. 1959, 1960; Ourecky 1975). The most well-known and deployed resistance gene, Ag_1, was originally found in red raspberry ‘Lloyd George’ and was used for more than 50 years in breeding programs (Daubeny 1966). However, an aphid biotype was discovered in the early 1990s that broke resistance conferred by Ag_1 (Daubeny and Anderson 1993). Ag_2 and Ag_3 are also dominant genes derived from red raspberry, specifically a wild *R. strigosus* population found in Ottawa, Canada, but unlike Ag_1, these genes were complementary and conferred only partial resistance (Daubeny and Stary 1982). The phenotypic similarities between the three genes has made it challenging to incorporate Ag_2 and Ag_3 reliably into new red raspberry cultivars (Dossett and Kempler 2012). Ag_4, Ag_5, and Ag_6 resistance genes come from *R. occidentalis* accessions collected from Maine and Michigan, USA, and Ontario, Canada. These three genes are of great interest because native genes are easier to integrate into breeding lines than red

Table 2. Red raspberry (*Rubus idaeus*) cultivars evaluated for spotted-wing drosophila (*Drosophila suzukii*) resistance.

Cultivar	PI no.	Fruiting type	Breeding program	Study
Cascade Delight	—	Floricane	Washington State University, Puyallup, WA, USA	Lee et al. (2011), Wöhner et al. (2021)
Centennial	PI 618456	Floricane	Washington State University, Puyallup, WA, USA; University of Idaho, Sandpoint, ID, USA; Oregon State University, Corvallis, OR, USA; US Department of Agriculture, Corvallis, OR, USA	Lee et al. (2011)
Coho	PI 618392	Primocane	Oregon State University, Corvallis, OR, USA; US Department of Agriculture, Corvallis, OR, USA	Lee et al. (2011)
Encore	PI 638282	Primocane	Cornell University, Geneva, NY, USA	Lee et al. (2011)
Malahat	PI 638206	Floricane	Pacific Agri-Food Research Centre of Agriculture and Agri-Food Canada	Lee et al. (2011)
Willamette	PI 553362	Floricane	US Department of Agriculture, Corvallis, OR, USA	Lee et al. (2011), Wöhner et al. (2021)
Autumn Britten	PI 653100	Primocane	Horticulture Research International, East Malling, Kent, UK	Burrack et al. (2013)
Caroline	PI 653101	Primocane	University of Maryland, College Park, MD, USA; Rutgers University, New Brunswick, NJ, USA; Virgina Polytechnic Institute and State University, Blackstone, VA, USA; University of Wisconsin-River Falls, River Falls, WI, USA	Burrack et al. (2013)
Joan J	—	Primocane	Medway Fruits, Kent, UK	Burrack et al. (2013)
NC 344	—	Floricane	North Carolina State University, Raleigh, NC, USA	Burrack et al. (2013)
Nantahala	—	Primocane	North Carolina State University, Raleigh, NC, USA	Burrack et al. (2013)
Nova	PI 553480	Primocane	Agriculture Canada, Kentville, Nova Scotia, Canada	Burrack et al. (2013)
Octavia	—	Floricane	—	Burrack et al. (2013)
NCTG-1	—	Floricane	—	Burrack et al. (2013)
Dorman Red	PI 553425	Floricane	Mississippi State University, Starkville, MS, USA	Wöhner et al. (2021)
Japanese Wineberry	—	Floricane	—	Wöhner et al. (2021)
Him BK33-122	—	Floricane	—	Wöhner et al. (2021)
Gelbe Gigant	—	Floricane	—	Wöhner et al. (2021)
Schwarze aus Brunn	—	Floricane	—	Wöhner et al. (2021)
Malling Promise	PI 553425	Floricane	Horticulture Research International, East Malling, Kent, UK	Wöhner et al. (2021)
Him BK33-85	—	Floricane	—	Wöhner et al. (2021)
Wei Rula	—	Floricane	—	Wöhner et al. (2021)
Him 14 30-128	—	Floricane	—	Wöhner et al. (2021)
Madawaska	PI 553376	Floricane	Agriculture Canada, Abbotsford, British Columbia, Canada	Wöhner et al. (2021)
Royalty	PI 553302	Floricane	Cornell University, Geneva, NY, USA	Wöhner et al. (2021)
Tula Magic	—	Floricane	Promo-Fruit Ltd., Rafz, Switzerland	Wöhner et al. (2021)
Himbo Star	—	Floricane	Promo-Fruit Ltd., Rafz, Switzerland	Wöhner et al. (2021)
Radziejowa	—	Floricane	—	Wöhner et al. (2021)
Schonemann	PI 553527	Floricane	University of Bonn, Bonn, Germany	Wöhner et al. (2021)
Rumiloba	—	Floricane	—	Wöhner et al. (2021)
Preussen	PI 553525	Floricane	University of Bonn, Bonn, Germany	Wöhner et al. (2021)
Oktavia	—	Floricane	—	Wöhner et al. (2021)
Rumla	—	Floricane	—	Wöhner et al. (2021)
Glen Ample	PI 689559	Floricane	Scottish Crop Research Institute	Wöhner et al. (2021)
Nootka	PI 553372	Floricane	Agriculture Canada, Abbotsford, British Columbia, Canada	Wöhner et al. (2021)
Loganberry	—	Floricane	—	Wöhner et al. (2021)
Rubaca	—	Floricane	Technical University of Munich, Munich, Germany	Wöhner et al. (2021)
Reflamba	—	Floricane	—	Wöhner et al. (2021)
Elida	—	Floricane	—	Wöhner et al. (2021)
Kozacka	—	Floricane	—	Wöhner et al. (2021)
Lloyd George	PI 643942	Floricane	—	Wöhner et al. (2021)
Sugana	—	Floricane	Lubera Ag, Buchs, Switzerland	Wöhner et al. (2021)
Tulameen	PI 618441	Floricane	Agriculture Canada, Abbotsford, British Columbia, Canada	Wöhner et al. (2021)
Malling Freya		Floricane	Horticulture Research International, East Malling, Kent, UK	Wöhner et al. (2021)
Meeker	PI 553384	Floricane	Washington State University, Puyallup, WA, USA	Wöhner et al. (2021)
Sanibelle	—	Floricane	Technical University of Munich, Munich, Germany	Wöhner et al. (2021)

(Continued on next page)

Table 2. (*Continued*)

Cultivar	PI no.	Fruiting type	Breeding program	Study
Sokolica	—	Floricane	—	Wöhner et al. (2021)
Gelbe Antwerpen	—	Floricane	—	Wöhner et al. (2021)
Pokusa	—	Primocane	Research Institute of Pomology and Floriculture, Brzezna, Poland	Wöhner et al. (2021)
Autumn First	—	Primocane	Lubera Ag, Buchs, Switzerland	Wöhner et al. (2021)
Amira (BP-1)	—	Primocane	Berryplant, Baselga di Pinè, Italy	Wöhner et al. (2021)
Himbo Top	—	Primocane	Promo-Fruit Ltd., Rafz, Switzerland	Burrack et al. (2013), Wöhner et al. (2021)
Autumn Best	—	Primocane	Lubera Ag, Buchs, Switzerland	Wöhner et al. (2021)
Heritage	—	Primocane	Cornell University, Geneva, NY, USA	Wöhner et al. (2021)
Fall Gold	PI 553507	Primocane	University of New Hampshire, Durham, NH, USA	Wöhner et al. (2021)
Aroma Queen	—	Primocane	—	Wöhner et al. (2021)
Saxa Record	—	Primocane	—	Wöhner et al. (2021)
Goldmarie	—	Primocane	—	Wöhner et al. (2021)
Polana	PI 653106	Primocane	Research Institute of Pomology and Floriculture, Brzezna, Poland	Wöhner et al. (2021)
Kweli	—	Primocane	Advanced Berry Breeding, Hedel, Netherlands	Wöhner et al. (2021)
Golden Everest	—	Primocane	—	Wöhner et al. (2021)
Autumn Bliss	PI 553325	Primocane	Horticulture Research International, East Malling, Kent, UK	Wöhner et al. (2021)
Gelbe Siebenkugel	—	Primocane	—	Wöhner et al. (2021)
Ruby Fall	—	Primocane	—	Wöhner et al. (2021)
Kwanza	—	Primocane	Advanced Berry Breeding, Hedel, Netherlands	Wöhner et al. (2021)
Enrosadira	—	Primocane	Molari Berries & Breeding, Cesena, Italy	Wöhner et al. (2021)
Zefa 3	—	Primocane	—	Wöhner et al. (2021)
Poranna Rosa	—	Primocane	Research Institute of Pomology and Floriculture, Brzezna, Poland	Wöhner et al. (2021)
Regina	—	Primocane	Berryplant, Baselga di Pinè, Italy	Wöhner et al. (2021)
Mapema	—	Primocane	Advanced Berry Breeding, Hedel, Netherlands	Wöhner et al. (2021)
Polka	—	Primocane	Research Institute of Pomology and Floriculture, Brzezna, Poland	Wöhner et al. (2021)
Fallred Streib	—	Primocane	—	Wöhner et al. (2021)

raspberry resistance genes. Introgression from red raspberry involves several generations of backcrossing to reconstitute the black raspberry fruit phenotype from the "purple hybrids" that result from black raspberry and red raspberry crosses (Dossett and Finn 2010). Ag_6 had similar phenotypic responses as Ag_4 and requires further investigation to determine its novelty (Dossett and Finn 2010).

Wild *R. strigosus* accessions have been of significant interest because these plants have demonstrated resistance to the aphid and are the source of Phytophthora root rot resistance in red raspberry cultivars such as 'Newburgh' and 'Latham' (Daubeny and Stary 1982; Daubeny et al. 1992). Accessions of *R. idaeus*, *R. spectabilis*, *R. crataegifolius*, and *R. parviflorus* also have aphid resistance (Daubeny et al. 1992). The details of these resistance sources remain vague and have not yet been compared with previously identified resistance genes. Although these sources may have underutilized resistance, incorporating these genetics presents additional challenges, including limited diversity, varying degrees of hybrid compatibility with *R. idaeus* or *R. occidentalis*, and the incorporation of undesirable wild traits following successful interspecific hybridization.

Additional research into the resistance mechanisms of these genes may aid breeding efforts. Aphid resistance has been characterized as either antixenosis resistance (affects feeding and alters insect behavior), antibiosis resistance (affects biotic potential of the insect such as fecundity)or tolerance (the plant's ability to remain economically vigorous in the face of infestation) (van Emden 2007). To date, Ag_1, Ag_4, Ag_5, and an undesignated resistance gene have been evaluated for their resistance mechanisms. Ag_1 demonstrated antixenosis, as did Ag_4 to Ag_6, making it difficult to distinguish each of these genes based on phenotype alone (Kennedy and Schaefers 1974; Lightle et al. 2012, 2015). Although still unclear, Ag_2 and Ag_3 may have more of an antibiotic mechanism, as small colonies of aphids were observed on these plants (Daubeny and Stary 1982). Similar observations of red raspberry 'Washington' were made by Kennedy and Schaefers (1974), who concluded that 'Washington' demonstrated antibiosis. 'Washington' is derived from a cross between 'Cuthbert', a chance seedling selected from the wild in the northeastern United States, likely derived from *R. strigosus*, and 'Lloyd George', a chance seedling selected from the wild in Scotland, likely derived from *R. idaeus*. It appears that 'Washington' did not inherit Ag_1 from 'Lloyd George', but potentially inherited genes such as Ag_2 and Ag_3 or uncharacterized genes from 'Cuthbert' (Kennedy and Schaefers 1974).

Table 3. *Rubus* spp. with published reference genomes.

Study	Species	Ploidy	Berry type	Cultivar	Genome size (Mb)
VanBuren et al. (2016)	*Rubus occidentalis*	2x	Black raspberry	ORUS 4115-3	243
VanBuren et al. (2018)	*R. occidentalis*	2x	Black raspberry	ORUS 4115-3	290
Jibran et al. (2018)	*R. occidentalis*	2x	Black raspberry	ORUS 4115-3	223.8
Wight et al. (2019)	*Rubus idaeus*	2x	Red raspberry	Joan J	300
Davik et al. (2022)	*R. idaeus*	2x	Red raspberry	Anitra	291.7
Price et al. (2023)	*R. idaeus*	2x	Red raspberry	Autumn Bliss	263
	R. idaeus	2x	Red raspberry	Malling Jewel	265.5
Worthington et al. (2020)	*Rubus ulmifolius*	2x	Blackberry	Burbank Thornless	341
	Rubus argutus	2x	Blackberry	Hillquist	314
Brůna et al. (2023)	*R. argutus*	2x	Blackberry	Hillquist	298
Paudel et al. (2025)	*Rubus* spp.	4x	Blackberry	Watson BL1 selection	247
Wang et al. (2021)	*Rubus chingii*	2x	Red raspberry	—	231.21

The development and deployment of molecular markers associated with each of these genes would be beneficial for breeders seeking to improve selection and combine multiple sources of resistance in future cultivars.

Improvements in Plant Breeding

Red and black raspberries and other caneberries are challenging to breed. They are labor-intensive with long breeding cycles and require significant time and resources per breeding cycle. Advances such as genomic selection and high-throughput phenotyping (HTP) may help to reduce investments, thus shortening the breeding cycle through improved selection and evaluation efficiency. Genomic and phenomic methodological advancements arise from the progress in genetic technologies as well as in drones, imaging, robotics, and artificial intelligence, which increase the affordability and availability of important tools to plant breeders. These technological improvements have been accompanied by the development of improved statistical methods, software, and computing infrastructure that facilitate the analysis of large "omics" datasets, leading to a better understanding of the genomes and genetic architecture of agricultural phenotypes.

Studies of genomic and phenomic methodologies for plant breeding are abundant for staple field crops such as corn (*Zea mays*) and wheat (*Triticum aestivum*). Marker-assisted breeding (MAB) and HTP, discussed here, are two techniques that interest plant breeders. Other such techniques, including genetic engineering, genome editing, speed breeding, and mutation breeding, have been reviewed in Elango et al. (2021). Some phenomic and genomic methodologies have begun to be implemented in raspberry breeding systems, but there are still many opportunities to study these techniques.

Caneberry Genetics and Genomics

Genome sequencing and targeted genotyping are critical for developing MAB capabilities and investigating the genetic basis of traits of interest. High-throughput sequencing has become increasingly affordable, making genetic and genomic analytic methods more accessible to horticultural and specialty crops. Only within the past two decades have these methods been used to examine traits that are breeding targets in specialty crops such as caneberries. Publication of genomic studies in caneberries has increased within the past decade. Genetic maps have been published from multiple red raspberry biparental populations using simple sequence repeats (SSRs), amplified fragment length polymorphisms (AFLPs), expressed sequence tags (ESTs), random amplified polymorphic DNA (RAPD), resistance gene analog polymorphisms, single nucleotide polymorphisms (SNPs), and EST-SSRs (Graham et al. 2002, 2004; Pattison et al. 2007; Ward et al. 2012). Studies using AFLPs and RAPD led the development of genetic maps because these marker types do not require a reference genome (Jiang 2013), which have only become available since 2016 (Table 3). The black raspberry genome was sequenced and assembled to chromosome scale, followed by red raspberry and blackberry (Bruna et al. 2023; Davik et al. 2022; Jibran et al. 2018; Paudel et al. 2025; Price et al. 2023; VanBuren et al. 2016, 2018; Wight et al. 2019; Worthington et al. 2020). A reference genome was also developed for a red raspberry native to Asia, *Rubus chingii* (Wang et al. 2021). Accurately assembled and annotated genome sequences enable downstream studies to identify genetic loci, develop and deploy molecular markers for targeted genotyping, map new traits, and accelerate cultivar development.

Linkage and association mapping are valuable techniques for elucidating the genomic loci controlling phenotypic variation for important commercial traits and supporting marker development for MAS. Linkage mapping generally uses one or more biparental populations to determine the recombination frequency of genetic markers and estimate the order and genetic distance between adjacent markers to produce a map (Collard et al. 2005). QTLs associated with traits of interest are then identified using several different statistical methods that, generally speaking, divide the study population into groups according to genotype at the locus of a marker of interest and evaluate these groups for a statistically significant difference for the trait of interest (Tanksley 1993). Unlike linkage mapping, which is limited to investigating the effects of alleles contained in one or more biparental populations, association mapping uses diverse populations to investigate the effects of a wider set of alleles representing a crop's broader germplasm base (i.e., one or more breeding programs) (Gupta et al. 2014). Both methodologies have their statistical challenges, but one of the greatest differences is the low resolution and high power of detection of linkage mapping vs. the high resolution and low power of association mapping, with association mapping potentially failing to detect the effects of important rare alleles present in only a handful of accessions (Rincent et al. 2014; Zhu et al. 2008).

Currently, linkage mapping studies predominate in caneberry, with only three reported association mapping studies, two for blackberry and one for raspberry (Chizk et al. 2023; Godwin 2021; Khadgi and Weber 2021). Multiple studies on genetic loci for agronomic traits, fruit and nutritional quality, and biotic and abiotic resistance traits have occurred for red raspberry using linkage and association mapping methods (Bushakra et al. 2013; Graham et al. 2006, 2011; Kassim et al. 2009; Khadgi and Weber 2021; Molina-Bravo et al. 2014; Sargent et al. 2007; Scolari et al. 2021; Simpson et al. 2017). Similar studies have also been conducted in black raspberry, although with fewer examples and none involving association mapping (Bradish et al. 2016a, 2016b; Bushakra et al. 2013, 2015, 2018; Willman et al. 2022).

Genomics-assisted Breeding in Caneberries

The most relevant genomic methods for raspberry cultivar development are MAS and genomic selection (GS), or genomic prediction. MAS and GS are commonly used to increase selection efficiency in breeding and to enable selection for specific traits during early stages of plant development. They have been used extensively in many of the staple crops, particularly wheat and corn (Bassi et al. 2016). MAS uses molecular markers such as SNPs that are closely linked to specific genes or mutations of interest to predict the presence and dosage of a desirable allele in parents or progeny (Ben-Ari and Lavi 2012). GS uses information from numerous genome-wide molecular markers to produce genomic estimated breeding values for a given trait based on a related training population, which is then deployed in wider populations (Meuwissen et al. 2001). MAS has thus far been demonstrated to be well suited for tracking and assessing traits that are qualitative or controlled by few genes, whereas GS is better suited for traits that are highly quantitative and polygenic (Bernardo 2008; Poland and Rutkoski 2016). In red raspberry, MAS has been researched minimally and limited to tracking *P. rubi* and RBDV resistance (Ward et al. 2012; Weber et al. 2008). These studies indicated that it could be a successful tool for breeders, but genetic background effects have prevented the developed markers from being widely implemented. Additional studies are needed to identify markers that can track these traits reliably. More recently, markers related to *P. rubi* resistance and fruit-quality traits were validated for their use in Scottish breeding programs (Graham et al. 2011; Jennings et al. 2016).

Research to develop molecular markers for selecting aphid resistance genes in black raspberry has begun and is becoming more of a reality as further genetic information is generated. Bushakra et al. (2015) developed the first linkage map for black raspberry and mapped the location of Ag_4 to chromosome 6 using the phenotypic marker Ag4_AphidR. Bushakra et al. (2018) later mapped Ag_5 and the unnamed gene with this same linkage map and developed potential molecular markers. The primers designed for these markers were SSRs and high-resolution melting (HRM) markers. Of the 93 primers tested, four were associated with resistance in a validation set of parents and three resistant and three susceptible progeny from 16 families. An HRM marker, S99_122915_HRM, differentiated resistant individuals from susceptible ones regardless of source (Fig. 8). An SSR marker, S99_13262, and a presence/absence marker after agarose gel electrophoresis, S525_111520_gel, identified resistant individuals with the unnamed or Ag_4 resistance sources. Another SSR marker, S99_476941, was specific to the Ag_5 source. None of the identified markers could distinguish between the Ag_4 and unnamed sources of resistance. Given the limited size of the validation population, Bushakra et al. (2018) recommended first testing these primers

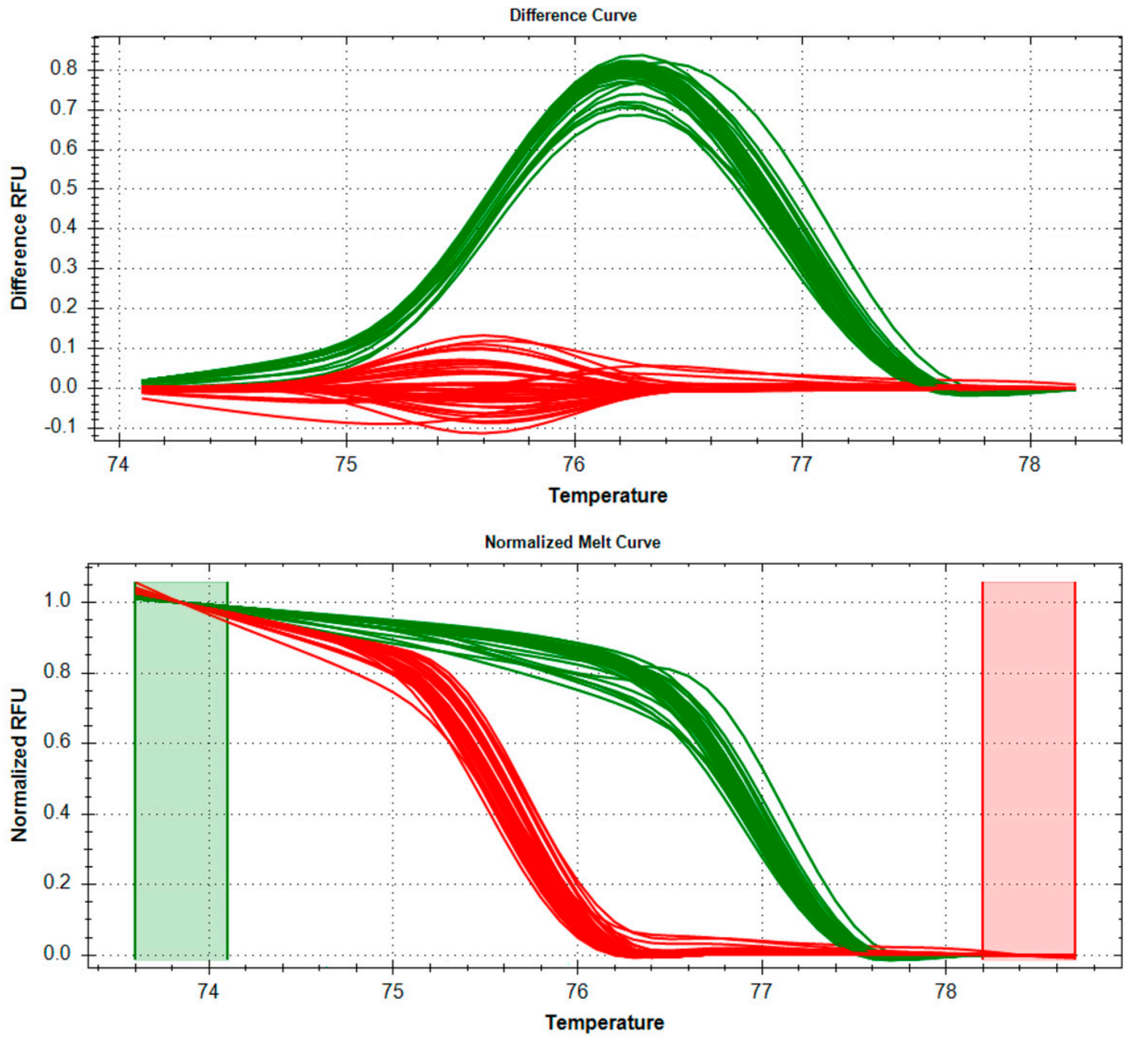

Fig. 8. Difference melt curves (**top**) and normalized melt curves (**bottom**) produced using the high-resolution melting (HRM) marker S99_122915_HRM. Green curves correspond to plants carrying at least one resistance gene whereas red curves correspond to susceptible plants. Figures courtesy of Nahla Bassil and Ryan King, US Department of Agriculture–Agricultural Research Service. RFU = relative fluorescence units.

on parents before using them to evaluate progeny. The USDA-ARS HCPGIRU breeding program has used the HRM marker routinely to screen black raspberry seedlings for aphid resistance. Most recently, Mulch (2021) conducted differential gene expression analysis using the whole-leaf transcriptomes of genetically resistant and susceptible progeny from three black raspberry mapping populations, each containing one of the three sources of resistance found by Dossett and Finn (2010)—*Ag₄*, *Ag₅*, and the undesignated resistance gene—in response to inoculation with aphids. Their study found various significantly DEGs across each of the mapping populations. In the mapping population with *Ag₄*, significant DEGs were found on chromosomes 2, 3, 4, and 6. The mapping population with *Ag₅* had significant DEGs observed on chromosomes 1, 2, 4, 5, 6, and 7. The final population with the undesignated resistance gene had significant DEGs on chromosomes 1, 2, 3, 6, and 7. The occurrence of significant DEGs on chromosome 6 provides additional support for the presence of these resistance genes on chromosome 6 (Bushakra et al. 2015, 2018). Mulch (2021) suggested that the other genes may be associated with general stress response genes. By combining the information obtained by Bushakra et al. (2015, 2018) and Mulch (2021), the location of *Ag₄*, *Ag₅*, and the undesignated resistance gene can be mapped with greater precision and can aid in the development of more efficient molecular markers that can be used by plant breeders to target each locus/gene and to combine (or "pyramid") multiple sources of resistance.

To date, there have been no studies investigating the use of GS in red raspberry breeding programs. Successful development and deployment of these methods would benefit caneberry breeders significantly who are still relying predominantly on traditional methods for trait selection. This is particularly true for traits caused by pests and pathogens such as *P. penetrans*, the resistance mechanisms of which appear to be quantitative, and the effects of which may not fully manifest during the earliest years of plant development.

Phenomics Methods in Caneberries

HTP can be important to plant breeders because these technologies enable rapid data collection and characterization of traits of interest in large populations. HTP can include imaging and environmental sensors, although investigations and development of data processing procedures for imaging are discussed most heavily in the literature (Shakoor et al. 2017). Like genotyping, costs for HTP have declined in the past 10 years, making these technologies more accessible.

High-throughput imaging can reduce the effects of human bias and the time spent phenotyping material. This is particularly helpful for traits that require time-intensive or destructive assessments. These imaging systems have variable setups and sensors capable of recording data across infrared (IR) and visible light spectra (Shakoor et al. 2017). The raw data produced are generally not useful as traditional phenotypic measurements, but can be converted by mathematical modeling into relevant metrics for assessing plant characteristics and performance (Kior et al. 2021). Some of the prominent technologies for automated field-based imaging include mounted ground-based systems, unmanned aerial vehicles, and satellites.

To date, there have been few studies that have investigated or used HTP in red raspberry production. Williams et al. (2017) described a design for a mounted ground-based system capable of imaging maturing canes of red raspberry with shortwave IR and visible and near-IR sensors. This system involved a tractor that drove along the rows pulling a trolley mounted with the sensors that captured side images of the plants, which were used to determine whether this method could accurately segment individual plants with hyperspectral imaging (Williams et al. 2017). Their results ultimately demonstrated they could, and this was the first report on ground-based segmentation for a bush crop. It was used again successfully to determine whether spectral data could be used with an existing linkage map and genetic markers for analyzing QTLs associated with desired biologic traits (Williams et al. 2021). Although its cost-effectiveness for more obvious phenotypic traits could be argued, the spectral QTLs also collocated with identified QTLs of traits that are difficult to phenotype, such as root damage and root density. The correlation between these traits indicated that HTP-based imaging could be helpful in phenotyping for soilborne pathogens. This has been reinforced with a recent study by Williams et al. (2023), who used a hand trolley system for lateral imaging of plants experiencing different abiotic and biotic stresses in a greenhouse. Four treatments were tested on red raspberry plants in the study: two abiotic stress treatments of low water availability and high water availability, and two biotic stress treatments of *P. rubi* or vine weevil (*Otiorhynchus sulcatus*) infestations. The various spectral ratios examined demonstrated strong correlations to multiple biophysical traits associated with these stresses (Williams et al. 2023). One challenge was that the available methods were not helpful in delineating the causal stresses from one another, and caution was needed to avoid misidentifying the causal stress.

Other characteristics have been assessed with different sensing technologies in red raspberry. Shortly after the publication of the results of the work by Williams et al. (2017), Pavlovic et al. (2018) reported the use of a thermal camera to assess canopy temperatures of red raspberry experiencing different irrigation and mulching treatments. Many of the correlations using the crop water stress index derived from the spectral data, soil moisture, and yield data resembled the same correlations for these traits in other crops, suggesting that this method could be a suitable, efficient alternative for soil moisture measurements. A ground-based hyperspectral imaging system different from the ones used by Williams et al. (2017, 2021, 2023) was used by Jung et al. (2019) to evaluate the effects of shade cover types on yield and berry characteristics of several red raspberry cultivars. Jung et al. (2019) used an ASD FieldSpec® 3 MAX (Malvern Panalytical Ltd., Malvern, UK) and a Cubert UHD185 (Cubert, Ulm, Germany) to derive the photochemical reflectance index (PRI), water index, normalized nitrogen index, and normalized difference vegetation index (NDVI). Significant differences in PRIs were observed, but not in other indices in shade cover treatments. All red raspberry cultivars in the study had greater light utilization efficiency under shade than their unshaded counterparts. The initial results demonstrate the promise of using spectral data to assess red raspberry response to treatments.

In yet another imaging system, red raspberry berry shape and color were assessed using the automated PSI PlantScreen (TM) (Photon Systems Instruments, Drásov, Czech Republic) red, green, and blue (RGB) imaging system implemented by the University of Helsinki as part of a study on floricane yield and berry quality (Palonen et al. 2021). Seven cultivars were considered, and it was found that HTP was an effective tool for evaluating both berry shape and berry color, but not for evaluating berry weight. Palonen et al. (2021) predicted that the colorimetric data provided by HTP will become increasingly widespread in coming years for harvest and postharvest assessments. Similarly, Sudars et al. (2022) developed a deep neural network model for recognizing and classifying red raspberry buds, flowers, and berries at various development stages in the field using RGB images; they have since released the model for public use.

Recently, Manganaris et al. (2023) presented the first investigation of the use of aerial remote sensing with drones to predict flowering and harvesting of select red raspberry cultivars Kweli, Imara, and Wengi in Cyprus. Ground-based measurements with soil plant analysis development (SPAD) meters were also collected. Traditional phenotype data on cane and physiological characteristics were recorded. The vegetative indices NDVI, normalized difference red-edge index, and green NDVI were calculated from remote data. Preliminary data support that the superior performance of 'Kweli' could be correlated to higher chlorophyll levels recorded with the SPAD meter, stomatal conductance, and fluorescence efficiency.

Conclusion

Many historically prominent diseases and pests of red and black raspberry in the PNW have been key research and breeding objectives for regional breeding programs since their inception. Improving our understanding of the genetics for resistance and tolerance of these biotic stresses is essential for developing elite cultivars with resistance to multiple major pests and diseases. New studies involving genetic mapping, association mapping, and genomic prediction are required to produce low-cost marker assays for selecting sources of resistance within existing breeding pipelines. As legislation and public opinion around chemical management shifts, production environments change, and global demand for small fruit increases, managing these issues effectively and sustainably by breeding resistant cultivars will be critical for future production. Developments in genomic and phenomic technologies present an opportunity for breeders to provide growers with resilient cultivars and to address emerging challenges quickly. Evaluation and validation of these techniques for measuring biotic stress response in regional germplasm is needed before they can be implemented with confidence.

References Cited

Alfonso C, Raposo R, Melgarejo P. 2000. Genetic diversity in *Botrytis cinerea* populations on vegetable crops in greenhouses in south-eastern Spain. Plant Pathol. 49(2):243–251. https://doi.org/10.1046/j.1365-3059.2000.00452.x.

Asplen MK, Anfora G, Biondi A, Choi D-S, Chu D, Daane KM, Gibert P, Gutierrez AP, Hoelmer KA, Hutchison WD, Isaacs R, Jiang Z-L, Kárpáti Z, Kimura MT, Pascual M, Philips CR, Plantamp C, Ponti L, Vétek G, Vogt H, Walton VM, Yu Y, Zappalà L, Desneux N. 2015. Invasion biology of spotted wing Drosophila (*Drosophila suzukii*): A global perspective and future priorities. J Pest Sci. 88(3):469–494. https://doi.org/10.1007/s10340-015-0681-z.

Atwell S, Corwin JA, Soltis NE, Subedy A, Denby KJ, Kliebenstein DJ. 2015. Whole genome resequencing of *Botrytis cinerea* isolates identifies high levels of standing diversity. Front Microbiol. 6:996. https://doi.org/10.3389/fmicb.2015.00996.

Barbara DJ, Jones AT, Henderson SJ, Wilson SC, Knight VH. 1984. Isolates of *Raspberry bushy dwarf virus* differing in *Rubus* host range. Ann Appl Biol. 105(1):49–54. https://doi.org/10.1111/j.1744-7348.1984.tb02801.x.

Barnett OW, Murant AF. 1970. Host range, properties and purification of *Raspberry bushy dwarf virus*. Ann Appl Biol. 65(3):435–449. https://doi.org/10.1111/j.1744-7348.1970.tb05512.x.

Barritt BH. 1971. Fruit rot susceptibility of red raspberry cultivars. Plant Dis Rep. 55(2):135–139.

Barritt BH, Crandall PC, Bristow PR. 1979. Breeding for root rot resistance in red raspberry. J Am Soc Hortic Sci. 104(1):92–94. https://doi.org/10.21273/JASHS.104.1.92.

Barritt BH, Crandall PC, Bristow PR. 1981. Red raspberry clones resistant to root rot. Fruit Var J. 35(2):60–62.

Bassi FM, Bentley AR, Charmet G, Ortiz R, Crossa J. 2016. Breeding schemes for the implementation of genomic selection in wheat (*Triticum* spp.). Plant Sci. 242:23–36. https://doi.org/10.1016/j.plantsci.2015.08.021.

Bellamy DE, Sisterson MS, Walse SS. 2013. Quantifying host potentials: Indexing postharvest fresh fruits for spotted wing Drosophila, *Drosophila suzukii*. PLoS One. 8(4):e61227. https://doi.org/10.1371/journal.pone.0061227.

Ben-Ari G, Lavi U. 2012. Marker-assisted selection in plant breeding, p 163–184. In: Altman A, Hasegawa PM (eds). Plant biotechnology and agriculture: Prospects for the 21st century. Elsevier, Amsterdam, the Netherlands. https://doi.org/10.1016/B978-0-12-381466-1.00011-0.

Bernardo R. 2008. Molecular markers and selection for complex traits in plants: Learning from the last 20 years. Crop Sci. 48(5):1649–1664. https://doi.org/10.2135/cropsci2008.03.0131.

Bradish CM, Bushakra JM, Dossett M, Bassil NV, Finn CE, Fernandez GE. 2016a. Genotyping and phenotyping heat tolerance in black raspberry (*Rubus occidentalis* L.). Acta Hortic. 1127:321–324. https://doi.org/10.17660/ActaHortic.2016.1127.50.

Bradish CM, Fernandez GE, Bushakra JM, Perkins-Veazie P, Dossett M, Bassil NV, Finn CE. 2016b. Evaluation of vigor and winter hardiness of black raspberry breeding populations (*Rubus occidentalis*) grown in the southeastern

US. Acta Hortic. 1133:129–134. https://doi.org/10.17660/ActaHortic.2016.1133.19.

Bristow PR, Barritt BH, McElroy FD. 1980. Reaction of red raspberry clones to the root lesion nematode. Acta Hortic. 112:39–46. https://doi.org/10.17660/ActaHortic.1980.112.5.

Brůna T, Aryal R, Dudchenko O, Sargent DJ, Mead D, Buti M, Cavallini A, Hytönen T, Andrés J, Pham M, Weisz D, Mascagni F, Usai G, Natali L, Bassil N, Fernadez GE, Lomsadze A, Armour M, Olukolu B, Poorten T, Britton C, Davik J, Ashrafi H, Aiden EL, Borodovsky M, Worthington M. 2023. A chromosome-length genome assembly and annotation of blackberry (Rubus argutus, cv. Hillquist). G3 (Bethesda). 13(20):jkac289. https://doi.org/10.1093/g3journal/jkac289.

Bulger MA, Stace-Smith R, Martin RR. 1990. Transmission and field spread of *Raspberry bushy dwarf virus*. Plant Dis. 74(7):514–517. https://doi.org/10.1094/PD-74-0514.

Burrack HJ, Fernandez GE, Spivey T, Kraus DA. 2013. Variation in selection and utilization of host crops in the field and laboratory by *Drosophila suzukii* Matsumara (Diptera: Drosophilidae), an invasive frugivore. Pest Manag Sci. 69(10):1173–1180. https://doi.org/10.1002/ps.3489.

Bushakra JM, Alice LA, Carter KA, Dossett M, Lee JC, Liston A, Meiers R, Mulch C, Nyberg AM, Peterson ME, Clark M, Vining KJ, Worthington ML, Yin MH, Sutherland BL, Zurn JD, Clark JR, Finn CE, Bassil NV, Hummer KE. 2020. Status of *Rubus* germplasm at the US National Clonal Germplasm Repository in Corvallis, Oregon. Acta Hortic. 1277:121–128. https://doi.org/10.17660/ActaHortic.2020.1277.17.

Bushakra JM, Bassil NV, Weiland JE, Finn CE, Vining KJ, Filichkin S, Dossett M, Bryant DW, Mocker TC. 2016. Comparative RNA-seq for the investigation of tolerance to Verticillium wilt in black raspberry. Acta Hortic. 1133:103–114. https://doi.org/10.17660/ActaHortic.2016.1133.16.

Bushakra JM, Bryant DW, Dossett M, Vining KJ, VanBuren R, Gilmore BS, Lee J, Mockler TC, Finn CE, Bassil NV. 2015. A genetic linkage map of black raspberry (*Rubus occidentalis*) and the mapping of *Ag4* conferring resistance to the aphid *Amphorophora agathonica*. Theor Appl Genet. 128(8):1631–1646. https://doi.org/10.1007/s00122-015-2541-x.

Bushakra JM, Dossett M, Carter KA, Vining KJ, Lee JC, Bryant DW, VanBuren R, Lee J, Mockler TC, Finn CE, Bassil NV. 2018. Characterization of aphid resistance loci in black raspberry (*Rubus occidentalis*). Mol Breed. 38:83. https://doi.org/10.1007/s11032-018-0839-5.

Bushakra JM, Krieger C, Deng D, Stephens MJ, Allan AC, Storey R, Symonds VV, Stevenson D, McGhie T, Chagné D, Buck EJ, Gardiner SE. 2013. QTL involved in the modification of cyanidin compounds in black and red raspberry fruit. Theor Appl Genet. 126(3):847–865. https://doi.org/10.1007/s00122-012-2022-4.

Cadman CH. 1954. Studies in *Rubus* virus diseases: VI. Aphid transmission of Raspberry leaf mottle virus. Ann Appl Biol. 41(1):207–214.

Cadman CH. 1965. Filamentous viruses infecting fruit trees and raspberry and their possible mode of spread. Plant Dis Rep. 49(3):230–232.

Çağlayan K, Gazel M, Roumi V, Lamovsek J, Beber A, Pleško IM. 2023. Sweet cherry, a new host of *Raspberry bushy dwarf virus*. J Plant Pathol. 105(1):307–311. https://doi.org/10.1007/s42161-022-01257-1.

Carroll JE, Marshall PM, Mattoon NE, Weber CA, Loeb GM. 2023. The predation impact of ruby-throated hummingbird, *Archilochus colubris*, on spotted-wing Drosophila, *Drosophila suzukii*, in raspberry, *Rubus idaeus*. Crop Prot. 163:106116. https://doi.org/10.1016/j.cropro.2022.106116.

Castillo P, Volvas N. 2007. Pathogenicity of *Pratylenchus* species, p 325–354. In: Hunt DJ, Perry RN (eds). *Pratylenchus* (Nematoda: Pratylenchidae): Diagnosis, biology, pathogenicity and management. Brill Academic Publishers, Leiden, The Netherlands.

Chambers J. 1961. The production and maintenance of virus-free raspberry plants. J Hortic Sci. 36(1):48–54. https://doi.org/10.1080/00221589.1961.11513999.

Chizk TM, Clark JR, Johns C, Nelson L, Ashrafi H, Aryal R, Worthington ML. 2023. Front Plant Sci. 14:1182790. https://doi.org/10.3389/fpls.2023.1182790.

Choi M-Y, Tang SB, Ahn S-J, Amarasekare KG, Shearer P, Lee JC. 2017. Effect of non-nutritive sugars to decrease the survivorship of spotted wing Drosophila, *Drosophila suzukii*. J Insect Physiol. 99:86–94. https://doi.org/10.1016/j.jinsphys.2017.04.001.

Collard BCY, Jahufer MZZ, Brouwer JB, Pang ECK. 2005. An introduction to markers, quantitative trait loci (QTL) mapping and marker-assisted selection for crop improvement: The basic concepts. Euphytica. 142(1–2):169–196. https://doi.org/10.1007/s10681-005-1681-5.

Crandall PC. 1995. Insects and diseases, p 167–191. In: Gough RE (ed). Bramble production: The management and marketing of raspberries and blackberries. Food Products Press, New York, NY, USA.

Crane MB, Lawrence JC. 1931. Inheritance of sex, colour, and hairiness in the raspberry, *Rubus idaeus* L. J Genet. 24(2):243–255. https://doi.org/10.1007/BF02983857.

Credi R, Shier JL, Stace-Smith R. 1986. Occurrence of *Raspberry bushy dwarf virus* in native thimbleberry in British Columbia. Acta Hortic. 186:17–22. https://doi.org/10.17660/ActaHortic.1986.186.2.

Dale A, Moore PP, McNicol RJ, Sjulin TM, Burmistrov LA. 1993. Genetic diversity of red raspberry varieties throughout the world. J Am Soc Hortic Sci. 118(1):119–129. https://doi.org/10.21273/JASHS.118.1.119.

Darrow GM. 1937. Blackberry and raspberry improvement, p 496–533. In: Yearbook of Agriculture. US Department of Agriculture, United States Government Printing Office, Washington DC. https://archive.org/details/yoa1937/page/n1/mode/2up.

Dashwood EP, Fox RA. 1988. Infection of flowers and fruit of red raspberry by *Botrytis cinerea*. Plant Pathol. 37:423–430.

Daubeny HA. 1966. Inheritance of immunity in the red raspberry to the North American strain of the aphid, *Amphorophora rubi* Kltb. J Am Soc Hortic Sci. 88:346–351.

Daubeny HA. 1971. Self-fertility in red raspberry cultivars and selections. J Am Soc Hortic Sci. 96(5):588–591. https://doi.org/10.21273/JASHS.96.5.588.

Daubeny HA. 1987. A hypothesis for inheritance of resistance to cane *Botrytis* in red raspberry. HortScience. 22(1):116–119. https://doi.org/10.21273/HORTSCI.22.1.116.

Daubeny HA, Anderson A. 1991. 'Tulameen' red raspberry. HortScience. 26(10):1336–1338. https://doi.org/10.21273/HORTSCI.26.10.1336.

Daubeny HA, Anderson AK. 1993. Achievements and prospects: The British Columbia red raspberry breeding program. Acta Hortic. 352:285–294. https://doi.org/10.17660/ActaHortic.1993.352.41.

Daubeny H, Kempler C. 2003. 'Tulameen' red raspberry. J Am Pomol Soc. 57(2):42–44.

Daubeny HA, Pepin HS. 1969. Variations in susceptibility to fruit rot among red raspberry cultivars. Plant Dis Rep. 53(12):975–977.

Daubeny HA, Pepin HS. 1974. Variations among red raspberry cultivars and selections in susceptibility to the fruit rot causal organisms *Botrytis cinerea* and *Rhizopus* spp. Can J Plant Sci. 54(3):511–516. https://doi.org/10.4141/cjps74-086.

Daubeny HA, Pepin HS. 1981. Resistance of red raspberry fruit and canes to *Botrytis*. J Am Soc Hortic Sci. 106(4):423–426. https://doi.org/10.21273/JASHS.106.4.423.

Daubeny H, Pepin HS, Levesque CA. 1992. Breeding for resistance to aphids and root rot in red raspberry. Acta Hortic. 317:187–190. https://doi.org/10.17660/ActaHortic.1992.317.22.

Daubeny HA, Stary D. 1982. Identification of resistance to *Amphorophora agathonica* in the native North American red raspberry. J Am Soc Hortic Sci. 107(4):593–597. https://doi.org/10.21273/JASHS.107.4.593.

Davik J, Røen D, Lysøe E, Buti M, Rossman S, Alsheikh M, Aiden EL, Dudchenko O, Sargent DJ. 2022. A chromosome-level genome sequence assembly of the red raspberry (*Rubus idaeus* L.). PLoS One. 17(3):e0265096. https://doi.org/10.1371/journal.pone.0265096.

DeVetter LW, Watkinson S, Zasada IA, Weiland JE, Hesse C, Walters TW. 2018. Effectiveness of nontarped broadcast fumigation and root removal on root lesion nematode and *Fusarium* and *Pythium* species in a red raspberry system. Plant Health Prog. 19(2):168–175. https://doi.org/10.1094/PHP-01-18-0006-RS.

Dolan A, MacFarlane S, Jennings SN. 2018. Pathogens in raspberry and other *Rubus* spp, p 41–61. In: Graham J, Brennan R (eds). Raspberry. Springer, Cham. https://doi.org/10.1007/978-3-319-99031-6_4.

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

Dossett M, Finn CE. 2010. Identification of resistance to the large raspberry aphid in black raspberry. J Am Soc Hortic Sci. 135(5):438–444. https://doi.org/10.21273/JASHS.135.5.438.

Dossett M, Kempler C. 2012. Biotypic diversity and resistance to the raspberry aphid *Amphorophora agathonica* in Pacific northwestern North America. J Am Soc Hortic Sci. 137(6):445–451. https://doi.org/10.21273/JASHS.137.6.445.

Duncan JM, Kennedy DM. 1989. The effect of waterlogging on *Phytophthora* root rot of red raspberry. Plant Pathol. 38(2):161–168. https://doi.org/10.1111/j.1365-3059.1989.tb02129.x.

Elad Y, Williamson B, Tudzynski P, Delen N. (2004). *Botrytis* spp. and the disease they cause in agricultural system: An introduction, p 1–8. In: Elad Y, Williamson B, Tudzynski P, Delen N (eds). *Botrytis:* Biology, Pathology and Control. Springer, Dordrecht, the Netherlands. https://doi.org/10.1007/978-1-4020-2626-3_1.

Elango D, Sandoya G, Chopra S. 2021. Techniques and tools of modern plant breeding, p 17–26. In: Ricroch A, Chopra S, Kuntz M (eds). Plant biotechnology. Springer, Cham, Switzerland. https://doi.org/10.1007/978-3-030-68345-0_2.

Fejer SO, Spangelo LPS. 1974. Three generations of inbreeding and S_2 factorial test crosses in red raspberry cultivars. Can J Genet Cytol. 16(2):419–432. https://doi.org/10.1139/g74-044.

Fernández-Fernández F, Antanaviciute L, Knight VH, Dunwell JM, Battey NH, Sargent DJ. 2013. Genetics of resistance to *Amphorophora idaei* in red raspberry. Acta Hortic. 976:501–508. https://doi.org/10.17660/ActaHortic.2013.976.71.

Fillinger S. 2016. *Botrytis*: The fungus, the pathogen and its management in agricultural systems (1st ed). Springer, Cham, Switzerland. https://doi.org/10.1007/978-3-319-23371-0.

Finn CE, Clark JR. 2012. Blackberry, p. 151–190. In: Badenes ML, Byrne DH (eds). Fruit breeding. Springer, New York, NY, USA.

Finn CE, Hancock JF. 2008. Raspberries, p 359–392. In: Hancock JF (ed). Temperate fruit crop breeding. Springer, Dordrecht. https://doi.org/10.1007/978-1-4020-6907-9_12.

Finn CE, Kempler C, Moore PP. 2008. Raspberry cultivars: What's new? What's succeeding? Where are breeding programs headed? Acta Hortic. 777:33–40. https://doi.org/10.17660/ActaHortic.2008.777.1.

Fiola JA, Swartz HA. 1994. Inheritance of tolerance to *Verticillium albo-atrum* in raspberry. HortScience. 29(9):1071–1073. https://doi.org/10.21273/HORTSCI.29.9.1071.

Food and Agriculture Organization of the United Nations. n.d. Crops and livestock products. https://www.fao.org/faostat/en/#data/QCL. [accessed 1 May 2023].

Forge TA, Kempler C. 2009. Organic mulches influence population densities of root-lesion nematodes, soil health indicators, and root growth of red raspberry. Can J Plant Pathol. 31(2):241–249. https://doi.org/10.1080/07060660909507597.

Forge T, Kenney E, Hashimoto N, Neilsen D, Zebarth B. 2016. Compost and poultry manure as preplant soil amendments for red raspberry: Comparative effects on root lesion nematodes, soil quality, and risk of nitrate leaching. Agric Ecosyst Environ. 223:48–58. https://doi.org/10.1016/j.agee.2016.02.024.

Forge T, Walters T, Koch C. 2014. Use of composted dairy manure solids mulch for raspberry: Influences on soil nematode communities and N and P availability. Compost Sci Util. 22(4):230–241. https://doi.org/10.1080/1065657X.2014.930677.

Forge T, Zasada I, Pinkerton J, Koch C. 2012. Host status and damage potential of *Paratrichodorus renifer* and *Pratylenchus penetrans* (Nematoda) to blueberry (*Vaccinium* spp.). Can J Plant Pathol. 34(2):277–282. https://doi.org/10.1080/07060661.2012.689261.

Fournier E, Giraud T. 2008. Sympatric genetic differentiation of a generalist pathogenic fungus, *Botrytis cinerea*, on two different host plants, grapevine and bramble. J Evol Biol. 21(1):122–132. https://doi.org/10.1111/j.1420-9101.2007.01462.x.

Fournier E, Giraud T, Albertini C, Brygoo Y. 2005. Partition of the *Botrytis cinerea* complex in France using multiple gene genealogies. Mycologia. 97(6):1251–1267. https://doi.org/10.3852/mycologia.97.6.1251.

Fournier E, Giraud T, Loiseau A, Vautrin D, Estoup A, Solignac M, Cornuet J, Brygoo Y. 2002. Characterization of nine polymorphic microsatellite loci in the fungus *Botrytis cinerea* (Ascomycota). Mol Ecol Notes. 2(3):253–255. https://doi.org/10.1046/j.1471-8286.2002.00207.x.

Funt RC. 2013. Pest and disease management, p 133–155. In: Funt RC, Hall HK (eds). Raspberries. CAB International, Wallingford, UK.

Galinato S, DeVetter LW. 2016. 2015 Cost estimates of establishing and producing red raspberries in Washington (TB21). https://wpcdn.web.wsu.edu/cahnrs/uploads/sites/5/2016/09/TB21-Red-Raspberry-Ent-Budget-Workbook.xlsx. [accessed 4 Jun 2025].

Garfinkel AR, Coats KP, Sherry DL, Chastagner GA. 2019. Genetic analysis reveals unprecedented diversity of a globally-important plant pathogenic genus. Sci Rep. 9(1):6671. https://doi.org/10.1038/s41598-019-43165-y.

Gariepy TD, Abram PK, Adams C, Beal D, Beers E, Beetle J, Biddinger D, Brind'Amour G, Bruin A, Buffington M, Burrack H, Daane KM, Demchak K, Fanning P, Gillett A, Hamby K, Hoelmer K, Hogg B, Isaacs R, Johnson B, Lee JC, Levensen HK, Loeb G, Lovero A, Milnes JM, Park KR, Prade P, Regan K, Renkema JM, Rodriguez-Saona C, Neupane S, Jones C, Sial A, Smythman P, Stout A, Van Timmeren S, Walton VM, Wilson JK, Wang X. 2024. Widespread establishment of adventive populations of *Leptopilina japonica* (Hymenoptera, Figitidae) in North America and development of a multiplex PCR assay to identify key parasitoids of *Drosophila suzukii* (Diptera, Drosophilidae). Neobiota. 93:63–90. https://doi.org/10.3897/neobiota.93.121219.

Gigot J, Walters TW, Zasada IA. 2013. Impact and occurrence of *Phytophthora rubi* and *Pratylenchus penetrans* in commercial red raspberry (*Rubus idaeus*) fields in northwestern Washington. Int J Fruit Sci. 13(4):357–372. https://doi.org/10.1080/15538362.2013.748373.

Giraud T, Fortini D, Levis C, Leroux P, Brygoo Y. 1997. RFLP markers show genetic recombination in *Botryotinia fuckeliana* (*Botrytis cinerea*) and transposable elements reveal two sympatric species. Mol Biol Evol. 14(11):1177–1185. https://doi.org/10.1093/oxfordjournals.molbev.a025727.

Godwin CE. 2021. Genetic control of sweetness, acidity, and seediness in blackberry (masters thesis). University of Arkansas, Fayetteville, AR, USA.

Goodhue RE, Bolda M, Farnsworth D, Williams JC, Zalom FG. 2011. Spotted wing Drosophila infestation of California strawberries and raspberries: Economic analysis of potential revenue losses and control costs. Pest Manag Sci. 67(11):1396–1402. https://doi.org/10.1002/ps.2259.

Graham KA, Beck BR, Zasada IA, Scagel CF, Weiland JE. 2021. Growth, sporulation, and pathogenicity of the raspberry pathogen *Phytophthora rubi* under different moisture and temperature regimes. Plant Dis. 105(6):1791–1797. https://doi.org/10.1094/PDIS-12-23-2641-RE.

Graham J, Hackett CA, Smith K, Woodhead M, MacKenzie K, Tierney I, Cooke D, Bayer M, Jennings N. 2011. Towards an understanding of the nature of resistance to *Phytophthora* root rot in red raspberry. Theor Appl Genet. 123(4):585–601. https://doi.org/10.1007/s00122-011-1609-5.

Graham J, Jennings N. 2009. Raspberry breeding, p 233–248. In: Jain SM, Priyadarshan PM (eds). Breeding plantation tree crops: Temperate species. Springer, New York, NY, USA. https://doi.org/10.1007/978-0-387-71203-1_7.

Graham J, Smith K, MacKenzie K, Jorgenson L, Hackett C, Powell W. 2004. The construction of a genetic linkage map of red raspberry (*Rubus idaeus* subsp. *idaeus*) based on AFLPs, genomic-SSR and EST-SSR markers. Theor Appl Genet. 109(4):740–749. https://doi.org/10.1007/s00122-004-1687-8.

Graham J, Smith J, Tierney I, Mackenzie K, Hackett CA. 2006. Mapping gene *H* controlling cane pubescence in raspberry and its association with resistance to cane *Botrytis* and spur blight, rust and cane spot. Theor Appl Genet. 112(5):818–831. https://doi.org/10.1007/s00122-005-0184-z.

Graham J, Smith K, Woodhead M, Russell J. 2002. Development and use of simple sequence repeat (SSR) markers in *Rubus* species. Mol Ecol Notes. 2(3):250–252. https://doi.org/10.1046/j.1471-8286.2002.00203.x.

Gupta PK, Kulwal PL, Jaiswal V. 2014. Association mapping in crop plants: Opportunities and challenges. Adv Genet. 85:109–147. https://doi.org/10.1016/B978-0-12-800271-1.00002-0.

Hahn M. 2014. The rising threat of fungicide resistance in plant pathogenic fungi: *Botrytis* as a case study. J Chem Biol. 7(4):133–141. https://doi.org/10.1007/s12154-014-0113-1.

Halgren A, Tzanetakis IE, Martin RR. 2007. Identification, characterization, and detection of *Black raspberry necrosis virus*. Phytopathology. 97(1):44–50. https://doi.org/10.1094/PHYTO-97-0044.

Hall HK. 1990. Blackberry breeding, p 249–312. In: Janick J (ed). Plant breeding reviews. Timber Press, Portland, OR, USA.

Hall HK, Hummer KE, Jamieson AR, Jennings SN, Weber CA. 2009. Raspberry breeding and genetics, p 39–353. In: Janick J (ed). Plant breeding reviews (vol 32). Wiley-Blackwell, Hoboken, NJ, USA. https://doi.org/10.1002/9780470593806.ch2.

Hall HK, Kempler C. 2011. Raspberry breeding. Fruit Veg Cereal Sci Biotechnol. 5(1):44–62.

Hall HK, Stanley CJ, Stephens MJ. 2005. *Rubus* in warm temperate and sub-tropical conditions: Production systems and genetic potential for new cultivars. Acta Hortic. 694:91–96. https://doi.org/10.17660/ActaHortic.2005.694.11.

Harshman JM, Jurick WM, Lewers KS, Wang SY, Walsh CS. 2014. Resistance to *Botrytis cinerea* and quality characteristics during storage of raspberry genotypes. HortScience. 49(3):311–319. https://doi.org/10.21273/HORTSCI.49.3.311.

Hedrick UP. 1925. The Small Fruits of New York. Report of the New York State Agricultural Experiment Station. Albany, NY, USA.

Heiberg N. 1995. Control of root rot of red raspberries caused by *Phytophthora fragariae* var. *rubi*. Plant Pathol. 44:153–159.

Heiberg N. 1999. Effects of raised beds, black soil mulch and oxadixyl on root rot (*Phytophthora fragariae* var. *rubi*) in red raspberry. Acta Hortic. 505:249–258. https://doi.org/10.17660/ActaHortic.1999.505.32.

Hill AR. 1956. Observations on the North American form of *Amphorophora rubi* Kalt. (Homoptera, Aphididae). Can Entomol. 88(2):89–91. https://doi.org/10.4039/Ent8889-2.

Hu MJ, Dowling ME, Schnabel G. 2018. Genotypic and phenotypic variations in *Botrytis* spp. isolates from single strawberry flowers. Plant Dis. 102(1):179–184. https://doi.org/10.1094/PDIS-06-17-0891-RE.

Hummer K, Hall HK. 2013. Raspberries, p 1–19. In: Funt RC, Hall HK (eds). Raspberries. CABI, Wallingford, UK.

International Committee on Taxonomy of Viruses. 2011. Genus: *Idaeovirus*, p 1173–1174. In: King AMQ, Adams MJ, Carstens EB, Lefkowitz EJ (eds). Virus taxonomy: Ninth report of the International Committee on Taxonomy of Viruses. Elsevier, Amsterdam, Netherlands. https://doi.org/10.1016/B978-0-12-384684-6.00100-2.

Jean-Gilles D, Li L, Ma H, Yuan T, Chichester CO, III, Seeram NP. 2012. Anti-inflammatory effects of polyphenolic-enriched red raspberry extract in an antigen-induced arthritis rat model. J Agric Food Chem. 60(23):5755–5762. https://doi.org/10.1021/jf203456w.

Jennings DL. 1983. Inheritance of resistance to *Botrytis cinerea* and *Didymella applanata* in canes in *Rubus idaeus*, and relationships between these resistances. Euphytica. 32(3):895–901. https://doi.org/10.1007/BF00042171.

Jennings DL. 1988. Raspberries and blackberries: Their breeding, diseases and growth. Academic Press, San Diego, CA, USA.

Jennings DL, Brydon E. 1989. Further studies on breeding for resistance to *Botrytis cinerea* in red raspberry canes. Ann Appl Biol. 115(3):507–513. https://doi.org/10.1111/j.1744-7348.1989.tb06571.x.

Jennings DL, Carmichael E. 1975. Resistance to grey mould (*Botrytis cinerea* Fr.) in red raspberry fruits. Hortic Res. 14:109–115.

Jennings SN, Graham J, Ferguson L, Young V. 2016. New developments in raspberry breeding in Scotland. Acta Hortic. 1133:23–28. https://doi.org/10.17660/ActaHortic.2016.1133.4.

Jennings DL, Jones AT. 1989. Further studies on the occurrence and inheritance of resistance in red raspberry to a resistance-breaking strain of *Raspberry bushy dwarf virus*. Ann Appl Biol. 114(2):317–323. https://doi.org/10.1111/j.1744-7348.1989.tb02108.x.

Jennings SN. 2018. Advances in *Rubus* breeding, p 17–28. In: Graham J, Brennan R (eds). Raspberry. Springer, Cham. https://doi.org/10.1007/978-3-319-99031-6_2.

Jennings DL, Williamson B. 1982. Resistance to *Botrytis cinerea* in canes of *Rubus idaeus* and some related species. Ann Appl Biol. 100:375–381.

Jevremović D, Paunović S. 2011. *Raspberry bushy dwarf virus*: A grapevine pathogen in Serbia. Pestic Fitomed. 26(1):55–60. https://doi.org/10.2298/PIF1101055J.

Jiang G-L. 2013. Molecular markers and marker-assisted breeding in plants. In: Andersen SB (ed). Plant breeding from laboratories to fields. IntechOpen, London, UK. https://doi.org/10.5772/52583.

Jibran R, Dzierzon H, Bassil N, Bushakra JM, Edger PP, Sullivan S, Finn CE, Dossett M, Vining KJ, VanBuren R, Mockler TC, Liachko I, Davies KM, Foster TM, Chagné D. 2018. Chromosome-scale scaffolding of the black raspberry (*Rubus occidentalis* L.) genome based on chromatin interaction data. Hortic Res. 5(8):8. https://doi.org/10.1038/s41438-017-0013-y.

Jones AT. 1979. The effects of *Black raspberry necrosis* and *Raspberry bushy dwarf viruses* in Lloyd George raspberry and their involvement in raspberry bushy dwarf disease. J Hortic Sci. 54(4):267–272. https://doi.org/10.1080/00221589.1979.11514880.

Jones MGK, Fosu-Nyarko J. 2014. Molecular biology of root lesion nematodes (*Pratylenchus* spp.) and their interaction with host plants. Ann Appl Biol. 164(2):163–181. https://doi.org/10.1111/aab.12105.

Jones JT, Haegeman A, Danchin EGJ, Gaur HS, Helder J, Jones MGK, Kikuchi T, Manzanilla-López R, Palomares-Rius JE, Wesemael WML, Perry RN. 2013. Top 10 plant-parasitic nematodes in molecular plant pathology. Mol Plant Pathol. 14(9):946–961. https://doi.org/10.1111/mpp.12057.

Jones AT, McGavin WJ, Geering ADW, Lockhart BEL. 2002. Identification of Rubus yellow net virus as a distinct badnavirus and its detection by PCR in *Rubus* species and in aphids. Ann Appl Biol. 141:1–10.

Jones AT, Murant AF, Jennings DL, Wood GA. 1982. Association of *Raspberry bushy dwarf virus* with raspberry yellows disease: Reaction of *Rubus* species and cultivars, and the inheritance of resistance. Ann Appl Biol. 100(1):135–147. https://doi.org/10.1111/j.1744-7348.1982.tb07200.x.

Jung A, Vohland M, Magyar M, Kovács L, Jung T, Péterfalvi Keller B, Sillinger F, Rák R, Szalay K. 2019. Snapshot hyperspectral imaging for field data acquisition in agriculture (in raspberry plantation). J Photogram Rem Sens Geoinform Sci. 28:196–202.

Kassim A, Poette J, Paterson A, Zait D, McCallum S, Woodhead M, Smith K, Hackett C, Graham J. 2009. Environmental and seasonal influences on red raspberry anthocyanin antioxidant contents and identification of quantitative traits loci (QTL). Mol Nutr Food Res. 53(5):625–634. https://doi.org/10.1002/mnfr.200800174.

Keep E. 1976. Progress in *Rubus* breeding at East Malling. Acta Hortic. 60:123–128. https://doi.org/10.17660/ActaHortic.1976.60.16.

Keep E. 1989. Breeding red raspberry for resistance to disease and pests. Plant Breed Rev. 6:245–321.

Keep E, Knight VH, Parker JH. 1977. *Rubus coreanus* as a donor of resistance to cane diseases and mildew in red raspberry breeding. Euphytica. 26(2):505–510. https://doi.org/10.1007/BF00027019.

Kennedy GG, Schaefers GA. 1974. Evidence for nonpreference and antibiosis in aphid-resistant red raspberry cultivars. Environ Entomol. 3(5):773–777. https://doi.org/10.1093/ee/3.5.773.

Kempler C, Hall HK. 2013. World raspberry production and marketing: Industry changes and trends from 1960 to 2010, p 213–233. In: Funt RC, Hall HK (eds). Raspberries. CABI, Wallingford, UK.

Kempler C, Muehlchen AM, Forge TA. 2012. Screening for resistance to *Phytophthora* root rot in raspberries: Identifying new sources of resistance. Acta Hortic. 926:59–64. https://doi.org/10.17660/ActaHortic.2012.926.6.

Khadgi A, Weber CA. 2021. Genome-wide association study (GWAS) for examining the genomics controlling prickle production in red raspberry (*Rubus idaeus* L.). Agronomy. 11(1):27. https://doi.org/10.3390/agronomy11010027.

Kichina VV. 1976. Raspberry breeding for mechanical harvesting in northern Russia. Acta Hortic. 60:89–94. https://doi.org/10.17660/ActaHortic.1976.60.12.

Kior A, Sukhov V, Sukhova E. 2021. Application of reflectance indices for remote sensing of plants and revealing actions of stressors. Photonics. 8(12):582. https://doi.org/10.3390/photonics8120582.

Knight VH. 1980a. Responses of red raspberry cultivars and selections to *Botrytis cinerea* and other fruit-rotting fungi. J Hortic Sci. 55(4):363–369. https://doi.org/10.1080/00221589.1980.11514947.

Knight VH. 1980b. Screening for fruit rot resistance in red raspberry at East Malling. Acta Hortic. 112:127–134. https://doi.org/10.17660/ActaHortic.1980.112.16.

Knight VH. 1991. Use of the salmonberry, *Rubus spectabilis* Pursh., in red raspberry breeding. J Hortic Sci. 66(5):575–581. https://doi.org/10.1080/00221589.1991.11516186.

Knight VH, Barbara DJ. 1981. Susceptibility of red raspberry varieties to *Raspberry bushy dwarf virus*. Euphytica. 30(3):803–811. https://doi.org/10.1007/BF00038809.

Knight RL, Briggs JB, Keep E. 1960. Genetics of resistance to *Amphorophora rubi* (Kalt.) in the raspberry: II. The gene *A2–A7* from the American variety, Chief. Genet Res. 1(2):319–331. https://doi.org/10.1017/S0016672300000288.

Knight VH, Fernández-Fernández F. 2008. Screening for resistance to *Phytophthora fragariae* var. *rubi* in *Rubus* germplasm at East Malling. Acta Hortic. 777:353–360. https://doi.org/10.17660/ActaHortic.2008.777.53.

Knight VH, Jennings DL, McNicol RJ. 1989. Progress in the UK raspberry breeding programme. Acta Hortic. 262:93–104. https://doi.org/10.17660/ActaHortic.1989.262.12.

Knight RL, Keep E, Briggs JB. 1959. Genetics of resistance to *Amphorophora rubi* (Kalt.) in the raspberry: I. The gene *A1* from Baumforth A. J Genet. 56(2):261–280. https://doi.org/10.1007/BF02984748.

Konstantinou S, Veloukas T, Leroch M, Menexes G, Hahn M, Karaoglanidis G. 2015. Population structure, fungicide resistance profile, and sdhB mutation frequency of *Botrytis cinerea* from strawberry and greenhouse-grown tomato in Greece. Plant Dis. 99(2):240–248. https://doi.org/10.1094/PDIS-04-14-0373-RE.

Kozhar O, Peever TL. 2018. How does *Botrytis cinerea* infect red raspberry? Phytopathology. 108(11):1287–1298. https://doi.org/10.1094/PHYTO-01-18-0016-R.

Lankes C. 1995. Elimination of *Raspberry bushy dwarf virus*. Acta Hortic. 385:70–75. https://doi.org/10.17660/ActaHortic.1995.385.8.

Lanning KK. 2014. Determining the time course of *Raspberry bushy dwarf virus* movement from pollination to systemic infection in red raspberry. (PhD Diss.). Washington State University, Pullman, WA, USA.

Lanning KK, Moore PP, Keller KE, Martin RR. 2016. First report of a resistance-breaking strain of *Raspberry bushy dwarf virus* in red raspberry (*Rubus idaeus*) in North America. Plant Dis. 100(4):868–868. https://doi.org/10.1094/PDIS-09-15-1011-PDN.

Lee JC, Bruck DJ, Curry H, Edwards D, Haviland DR, Van Steenwyk RA, Yorgey BM. 2011. The susceptibility of small fruits and cherries to the spotted-wing Drosophila, *Drosophila suzukii*. Pest Manag Sci. 67(11):1358–1367. https://doi.org/10.1002/ps.2225.

Lee JC, Wang X, Daane KM, Hoelmer KA, Isaacs R, Sial AA, Walton VM. 2019. Biological control of spotted-wing Drosophila (Diptera: Drosophilidae): Current and pending tactics. J Integr Pest Manag. 10(1):13. https://doi.org/10.1093/jipm/pmz012.

Leposavić A, Đurović D, Keserović Z, Popović B, Mitrović O, Miletić N, Magazin N. 2013. Evaluation of raspberry cultivars grown in the western Serbian region. Hortic Sci. 40(1):1–7. https://doi.org/10.17221/86/2012-HORTSCI.

Leroux P. 2007. Chemical control of *Botrytis* and its resistance to chemical fungicides, p 195–222. In: Elad Y, Williamson B, Tudzynski P, Delen N (eds). *Botrytis*: Biology, pathology and control. Springer, Dordrecht. https://doi.org/10.1007/978-1-4020-2626-3_12.

Leroux P, Fritz R, Debieu D, Albertini C, Lanen C, Bach J, Gredt M, Chapeland F. 2002. Mechanisms of resistance to fungicides in field strains of *Botrytis cinerea*. Pest Manag Sci. 58(9):876–888. https://doi.org/10.1002/ps.566.

Lightle DM, Dossett M, Backus EA, Lee JC. 2012. Location of the mechanism of resistance to *Amphorophora agathonica* (Hemiptera: Aphididae) in red raspberry. J Econ Entomol. 105(4):1465–1470. https://doi.org/10.1603/ec11405.

Lightle D, Dossett M, Ebert T, Finn CE, Martin RR, Lee JC. 2015. Effects of three novel resistant black raspberry selections on *Amphorophora agathonica* feeding behavior and performance. Arthropod-Plant Interact. 9(5):487–496. https://doi.org/10.1007/s11829-015-9390-z.

Ma Z, Michailides TJ. 2005. Genetic structure of *Botrytis cinerea* populations from different host plants in California. Plant Dis. 89(10): 1083–1089. https://doi.org/10.1094/PD-89-1083.

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

Maloney K, Pritts M, Wilcox W, Kelly MJ. 2005. Suppression of Phytophthora root rot in red raspberries with cultural practices and soil amendments. HortScience. 40(6):1790–1795. https://doi.org/10.21273/HORTSCI.40.6.1790.

Maloney KE, Wilcox WF, Sanford JC. 1993. Raised beds and metalaxyl for controlling Phytophthora root rot of raspberry. HortScience. 28(11):1106–1108. https://doi.org/10.21273/HORTSCI.28.11.1106.

Man In't Veld WA. 2007. Gene flow analysis demonstrates that *Phytophthora fragariae* var. *rubi* constitutes a distinct species, *Phytophthora rubi* comb. Mycologia. 99(2):222–226.

Manganaris G, Valanides N, Darra N, Papadopoulos G, Fountas S. 2023. The employment of remote and proximal sensing technologies to predict the flowering and harvesting periods of three red raspberry cultivars, p 27. In: Proceedings of the International Society of Horticulture Sciences XIII International Rubus and Ribes Symposium [Abstract], Portland, OR, USA.

Martin RR. 1998. Raspberry viruses in Oregon, Washington and British Columbia. Acta Hortic. 471:71–74. https://doi.org/10.17660/ActaHortic.1998.471.11.

Martin RR, Keller KE. 2021. Idaeoviruses (Mayoviridae), p 430–438. In: Bamford DH, Zuckerman M (eds). Encyclopedia of virology (4th ed, vol 3). Academic Press, Cambridge, MA, USA. https://doi.org/10.1016/B978-0-12-809633-8.21333-2.

Martin RR, Keller KE, Mathews H. 2001. Development of resistance to *Raspberry bushy dwarf virus* in 'Meeker'. Acta Hortic. 656:159–163.

Martin RR, MacFarlane S, Sabanadzovic S, Quito D, Poudel B, Tzanetakis I. 2013. Viruses and virus diseases of *Rubus*. Plant Dis. 97(2):168–182. https://doi.org/10.1094/PDIS-04-12-0362-FE.

Martin RR, Mathews H. 2001. Engineering resistance to *Raspberry bushy dwarf virus*. Acta Hortic. 551:33–38. https://doi.org/10.17660/ActaHortic.2001.551.4.

Martinez F, Blancard D, Lecomte P, Levis C, Dubos B, Fermaud M. 2003. Phenotypic differences between *vacuma* and *transposa* subpopulations of *Botrytis cinerea*. Eur J Plant Pathol. 109:479–488. https://doi.org/10.1023/A:1024222206991.

Martinez F, Dubos B, Fermaud M. 2005. The role of saprotrophy and virulence in the population dynamics of *Botrytis cinerea* in vineyards. Phytopathology. 95(6):692–700. https://doi.org/10.1094/PHYTO-95-0692.

Martínez JA, Valdés R, Vicente MJ, Bañón S. 2008. Phenotypical differences among *B. cinerea* isolates from ornamental plants. Commun Agric Appl Biol Sci. 73(2):121–129.

Mathew L, Tiffin H, Erridge Z, McLachlan A, Hunter D, Pathirana R. 2021. Efficiency of eradication of *Raspberry bushy dwarf virus* from infected raspberry (*Rubus idaeus*) by in vitro chemotherapy, thermotherapy, and cryotherapy and their combinations. Plant Cell Tiss Organ Cult. 144(1):133–141. https://doi.org/10.1007/s11240-020-01829-y.

Mavrič I, Viršček Marn M, Koron D, Žežlina I. 2003. First report of *Raspberry bushy dwarf virus* on red raspberry and grapevine in Slovenia. Plant Dis. 87(9):1148–1148. https://doi.org/10.1094/PDIS.2003.87.9.1148D.

Mavrič Pleško I, Viršček Marn M, Širca S, Urek G. 2009. Biological, serological and molecular characterization of *Raspberry bushy dwarf virus* from grapevine and its detection in the nematode *Longidorus juvenilis*. Eur J Plant Pathol. 123(3):261–268. https://doi.org/10.1007/s10658-008-9362-6.

Mayo MA, Jolly CA, Murant AF, Raschke JH. 1991. Nucleotide sequence of *Raspberry bushy dwarf virus* RNA-3. J Gen Virol. 72:469–472. https://doi.org/10.1099/0022-1317-72-2-469.

McGregor GR, Franz P. 2002. Field management of root rot in raspberries caused by *Phytophthora* spp. Acta Hortic. 585:293–297.

McIntosh H, Guédot C, Atucha A. 2023. Plastic mulches improve yield and reduce spotted-wing Drosophila in primocane raspberry. Sci Hortic. 320:112203. https://doi.org/10.1016/j.scienta.2023.112203.

Menzies GW. 1999. Crop profile for raspberries (red) in Washington. https://ipmdata.ipmcenters.org/documents/cropprofiles/WAraspberries-red.pdf. [accessed 15 Jan 2024].

Mercier J, Kong M. 2017. Verticillium wilt, p 56–58. In: Martin RR, Ellis MA, Williamson B, Williams RN (eds). Compendium of raspberry and blackberry diseases and pests (2nd ed). APS Press, St. Paul, MN, USA. https://doi.org/10.1094/9780890545720.002.

Meuwissen THE, Hayes BJ, Goddard ME. 2001. Prediction of total genetic value using genome-wide dense marker maps. Genetics. 157(4):1819–1829. https://doi.org/10.1093/genetics/157.4.1819.

Molina-Bravo R, Fernandez GE, Sosinski BR. 2014. Quantitative trait locus analysis of tolerance to temperature fluctuations in winter, fruit characteristics, flower color, and prickle-free canes in raspberry. Mol Breeding. 33(2):267–280. https://doi.org/10.1007/s11032-013-9947-4.

Montgomerie IG, Kennedy DM. 1980. The pathogenicity of *Phytophthora* species to red raspberry. Acta Hortic. 112:167–176. https://doi.org/10.17660/ActaHortic.1980.112.23.

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

Moore PP. 2004. 'Cascade Delight' red raspberry. HortScience. 39(1):185–187. https://doi.org/10.21273/HORTSCI.39.1.185.

Moore PP. 2006. 'Cascade Dawn' red raspberry. HortScience. 41(3):857–859. https://doi.org/10.21273/HORTSCI.41.3.857.

Moore PP, Daubeny HA. 1993. 'Meeker' red raspberry. Fruit Var J. 47(1):2–4.

Moore PP, Finn CE. 2007. 'Cascade Bounty' red raspberry. HortScience. 42(2):393–396. https://doi.org/10.21273/HORTSCI.42.2.393.

Moore P, Hoashi-Erhardt W. 2016. Raspberry breeding at Washington State University. Acta Hortic. 1133:45–48. https://doi.org/10.17660/ActaHortic.2016.1133.7.

Moore PP, Hoashi-Erhardt W, Finn CE, Martin RR, Dossett M. 2015. 'Cascade Harvest' red raspberry. HortScience. 50(4):624–627. https://doi.org/10.21273/HORTSCI.50.4.624.

Moore PP, Martin RR. 2008. Screening for resistance to *Raspberry bushy dwarf virus* via pollen transmission. Acta Hortic. 777:379–384. https://doi.org/10.17660/ActaHortic.2008.777.57.

Mulch C. 2021. Development of genetic resources for *Rubus occidentalis* from three segregating sources of resistance to aphid *Amphorophora agathonica* (masters' thesis). Oregon State University, Corvallis, OR, USA.

Murant AF, Chambers J, Jones AT. 1974. Spread of *Raspberry bushy dwarf virus* by pollination, its association with crumbly fruit, and problems of control. Ann Appl Biol. 77(3):271–281. https://doi.org/10.1111/j.1744-7348.1974.tb01403.x.

Murant AF, Jones AT, Jennings DL. 1982. Problems in the control of *Raspberry bushy dwarf virus*. Acta Hortic. 129:77–88. https://doi.org/10.17660/ActaHortic.1982.129.14.

Natsuaki T, Mayo MA, Jolly CA, Murant AF. 1991. Nucleotide sequence of *Raspberry bushy dwarf virus* RNA-2: A bicistronic component of a bipartite genome. J Gen Virol. 72:2183–2189. https://doi.org/10.1099/0022-1317-72-9-2183.

Nestby R, Heiberg N. 1995. Genetic variation for resistance to *Phytophthora fragariae* var. *rubi* in red raspberries. Euphytica. 81(2):143–149. https://doi.org/10.1007/BF00025426.

O'Dea JK. 2024. A review of *Agrilus cuprescens* (Ménétries, 1832), the rose stem girdler, in. North America. Agric For Entomol. 26:296–313.

O'Dea JK, Hill SE. 2022. Rose stem girdler emergence model. Washington State University AgWeatherNet, Prosser, WA, USA.

O'Dea JK, Milnes JM, Triapitsyn SV, Rugman-Jones PF. 2023. *Baryscapus rugglesi* (Rohwer, 1919) (Hymenoptera: Eulophidae) discovered in western North America: Redescription, notes on biology, and implications as a parasitoid of its host, *Agrilus cuprescens* (Ménétries, 1832) (Coleoptera: Buprestidae). Pan-Pac Entomol. 99(4):246–265.

Oregon Raspberry and Blackberry Commission. n.d. Why Oregon. https://oregon-berries.com/oregon/. [accessed 4 Aug 2023].

Ourecky DK. 1975. Brambles, p 98–129. In: Janick J, Moore JN (eds). Advances in fruit breeding. Purdue University Press, West Lafayette, IN, USA.

Ourecky DK, Slate GL. 1973. Jewel black raspberry. https://hdl.handle.net/1813/4819. [accessed 4 Jun 2025].

Overcash JP. 1972. Dormanred: A new variety for Mississippi. Miss Agric For Exp Stn Res Bull 365. https://scholarsjunction.msstate.edu/mafes-bulletins/365. [accessed 5 Jun 2025].

Pagán I, García-Arenal F. 2018. Tolerance to plant pathogens: Theory and experimental evidence. Int J Mol Sci. 19(3):810. https://doi.org/10.3390/ijms19030810.

Palonen P, Laine T, Mouhu K. 2021. Floricane yield and berry quality of seven primocane red raspberry (*Rubus idaeus* L.) cultivars. Sci Hortic. 285(27):110201. https://doi.org/10.1016/j.scienta.2021.110201.

Pattison JA, Samuelian SK, Weber CA. 2007. Inheritance of *Phytophthora* root rot resistance in red raspberry determined by generation means and molecular linkage analysis. Theor Appl Genet. 115(2):225–236. https://doi.org/10.1007/s00122-007-0558-5.

Paudel D, Peng Z, Parajuli S, Parrish SB, Deng Z. 2025. A chromosome-scale and haplotype-resolved genome assembly of tetraploid blackberry (*Rubus* L. subgenus *Rubus* Watson). Hortic Res. 12(6):uhaf052. https://doi.org/10.1093/hr/uhaf052.

Pavlovic M, Stricevic R, Cosic M, Djurovic N, Bogdan I. 2018. Irrigation and mulching effects on raspberry leaf temperatures measured by thermal imaging camera. Acta Hortic. 1197: 179–186. https://doi.org/10.17660/ActaHortic.2018.1197.24.

Pinkerton JN, Bristow PR, Windom GE, Walters TW. 2009. Soil solarization as a component of an integrated program for control of raspberry root rot. Plant Dis. 93(5):452–458. https://doi.org/10.1094/PDIS-93-5-0452.

Pinkerton JN, Ivors KL, Miller ML, Moore LW. 2000. Effect of soil solarization and cover crops on populations of selected soilborne plant pathogens in western Oregon. Plant Dis. 84(9):952–960. https://doi.org/10.1094/PDIS.2000.84.9.952.

Plants of the World Online. 2023. *Rubus* L. facilitated by the Royal Botanic Gardens, Kew. https://powo.science.kew.org/taxon/urn:lsid:ipni.org:names:30000199-2#children. [accessed 4 Aug 2023].

Poland J, Rutkoski J. 2016. Advances and challenges in genomic selection for disease resistance. Annu Rev Phytopathol. 54:79–98. https://doi.org/10.1146/annurev-phyto-080615-100056.

Polat İ, Baysal Ö, Mercati F, Gümrükcü E, Sülü G, Kitapcı A, Araniti F, Carimi F. 2018. Characterization of *Botrytis cinerea* isolates collected on pepper in South Turkey by using molecular markers, fungicide resistance genes and virulence assay. Infect Genet Evol. 60: 151–159. https://doi.org/10.1016/j.meegid.2018.02.019.

Price RJ, Davik J, Fernandéz-Fernandéz F, Bates HJ, Lynn S, Nellist CF, Buti M, Røen D, Šurbanovski N, Alsheikh M, Harrison RJ, Sargent DJ. 2023. Chromosome-scale genome sequence assemblies of the ‘Autumn Bliss’ and ‘Malling Jewel’ cultivars of the highly heterozygous red raspberry (*Rubus idaeus* L.) derived from long-read Oxford Nanopore sequence data. PLoS One. 18(5):e0285756. https://doi.org/10.1371/journal.pone.0285756.

Quito-Avila DF, Lightle D, Lee J, Martin RR. 2012. Transmission biology of *Raspberry latent virus*, the first aphid-borne reovirus. Phytopathology. 102(5):547–553. https://doi.org/10.1094/PHYTO-12-11-0331.

Quito-Avila DF, Lightle D, Martin RR. 2014. Effect of *Raspberry bushy dwarf virus*, *Raspberry leaf mottle virus*, and *Raspberry latent virus* on plant growth and fruit crumbliness in ‘Meeker’ red raspberry. Plant Dis. 98(2):176–183. https://doi.org/10.1094/PDIS-05-13-0562-RE.

Rankin WH. 1927. Mosaic of raspberries. New York State Agric Exp Stn Bull 543.

Rankin WH, Hockey JF. 1922. Mosaic and leaf curl (yellows) of the cultivated red raspberry. Phytopathology. 12(6):253–264.

Rincent R, Moreau L, Monod H, Kuhn E, Melchinger AE, Malvar RA, Moreno-Gonzalez J, Nicolas S, Madur D, Combes V, Dumas F, Altmann T, Brunel D, Ouzunova M, Flament P, Dubreuil P, Charcosset A, Mary-Huard T. 2014. Recovering power in association mapping panels with variables levels of linkage disequilibrium. Genetics. 197(1):375–387. https://doi.org/10.1534/genetics.113.159731.

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

Røen D, Davik J, Klemsdal S, Brurberg MB. 2012. ‘Asker’ as source of resistance to raspberry root rot. Acta Hortic. 946:139–141. https://doi.org/10.17660/ActaHortic.2012.946.20.

Rudolph RE, DeVetter LW. 2015. Management strategies for *Phytophthora rubi* and *Pratylenchus penetrans* in floricane red raspberry (*Rubus idaeus* L.). J Am Pomol Soc. 69(3): 118–136.

Rudolph RE, DeVetter LW, Benedict C, Zasada IA. 2019a. Raspberry growers’ perceptions and practices regarding soil quality, cover crops, and fumigation. HortTechnology. 29(4):482–489. https://doi.org/10.21273/HORTTECH04354-19.

Rudolph RE, Walters TW, DeVetter LW, Zasada IA. 2018. Contribution of a winter wheat cover crop to the maintenance of root lesion nematode populations in the red raspberry production system. HortTechnology. 28(2):182–188. https://doi.org/10.21273/HORTTECH03971-18.

Rudolph RE, Zasada IA, DeVetter LW. 2017. Annual and perennial alleyway cover crops vary in their effects on *Pratylenchus penetrans* in Pacific Northwest red raspberry (*Rubus idaeus*). J Nematol. 49(4):446–456. https://doi.org/10.21307/jofnem-2017-094.

Rudolph RE, Zasada IA, Hesse C, DeVetter LW. 2019b. Brassicaceous seed meal, root removal and chemical fumigation vary in their effects on soil quality parameters and *Pratylenchus penetrans* in a replanted floricane raspberry production system. Appl Soil Ecol. 133:44–51. https://doi.org/10.1016/j.apsoil.2018.08.024.

Sampson BJ, Werle CT, Stringer SJ, Adamczyk JJ. 2017. Ingestible insecticides for spotted wing Drosophila control: A polyol, Erythritol, and an insect growth regulator, Lufenuron. J Appl Entomol. 141(1–2):8–18. https://doi.org/10.1111/jen.12350.

Sapkota S, Burlakoti RR, Lamour K, Lubberts M, Punja ZK. 2022. Development and application of multiplex targeted-sequencing approaches to identify *Phytophthora* species associated with root rot and wilting complex of red raspberry. PLoS One. 17(11):e0275384. https://doi.org/10.1371/journal.pone.0275384.

Sapkota S, Burlakoti RR, Punja ZK. 2023a. Diversity in virulence and metalaxyl-m sensitivity of *Phytophthora rubi* isolates has implications for raspberry root rot and wilting complex management. Can J Plant Pathol. 45(3):263–276. https://doi.org/10.1080/07060661.2023.2175912.

Sapkota S, Burlakoti RR, Punja ZK, Gerbrandt EM. 2023b. Influence of cultivar, environmental conditions, and fungicides on the development of Phytophthora root rot and wilt on red raspberry. Crop Prot. 172:106347. https://doi.org/10.1016/j.cropro.2023.106347.

Sargent DJ, Fernández-Fernández F, Rys A, Knight VH, Simpson DW, Tobutt KR. 2007. Mapping of A_1 conferring resistance to the aphid *Amphorophora idaei* and *dw* (dwarfing habit) in red raspberry (*Rubus idaeus* L.) using AFLP and microsatellite markers. BMC Plant Biol. 7(1):15. https://doi.org/10.1186/1471-2229-7-15.

Scolari LM, Hancock RD, Hedley PE, Morris J, Smith K, Graham J. 2021. Combining QTL mapping and gene expression analysis to elucidate the genetic control of “crumbly” fruit in red raspberry (*Rubus idaeus* L.). Agronomy. 11(4):794. https://doi.org/10.3390/agronomy11040794.

Shakoor N, Lee S, Mockler TC. 2017. High-throughput phenotyping to accelerate crop breeding and monitoring of diseases in the field. Curr Opin Plant Biol. 38:184–192. https://doi.org/10.1016/j.pbi.2017.05.006.

Shi N, Chen F, Zhang X, Clinton SK, Tang X, Sun Z, Chen T. 2017. Suppression of oxidative stress and NFκB/MAPK signaling by lyophilized black raspberries for esophageal cancer prevention in rats. Nutrition. 9(4):413. https://doi.org/10.3390/nu9040413.

Shi N, Riedl KM, Schwartz SJ, Zhang X, Clinton SK, Chen T. 2016. Efficacy comparison of lyophilised black raspberries and combination of celecoxib and PBIT in prevention of carcinogen-induced oesophageal cancer in rats. J Funct Foods. 27:84–94. https://doi.org/10.1016/j.jff.2016.08.044.

Simpson CG, Cullen DW, Hackett CA, Smith K, Hallett PD, McNicol J, Woodhead M, Graham J. 2017. Mapping and expression of genes associated with raspberry fruit ripening and softening. Theor Appl Genet. 130(3):557–572. https://doi.org/10.1007/s00122-016-2835-7.

Špak J, Kubelková D. 2000. Epidemiology of *Raspberry bushy dwarf virus* in the Czech Republic. J Phytopathol. 148(6):371–377. https://doi.org/10.1046/j.1439-0434.2000.00513.x.

Staats M, van Baarlen P, van Kan JAL. 2005. Molecular phylogeny of the plant pathogenic genus *Botrytis* and the evolution of host specificity. Mol Biol Evol. 22(2):333–346. https://doi.org/10.1093/molbev/msi020.

Statistics Canada. 2023. Table 32-10-0364-01: Area, production and farm gate value of marketed fruits. https://www2.gov.bc.ca/gov/content/industry/agriculture-seafood/statistics/agriculture-and-seafood-statistics-publications. [accessed 4 Mar 2024]. [data set].

Stephens MJ, Buck EJ, Tahir J. 2016. Mapping potential resistance gene for *Raspberry bushy dwarf virus* in red raspberry. Acta Hortic. 1133:121–128. https://doi.org/10.17660/ActaHortic.2016.1133.18.

Stewart JE, Kroese D, Tabima JF, Larsen MM, Fieland VJ, Press CM, Zasada IA, Grünwald NJ. 2014. Pathogenicity, fungicide resistance, and genetic variability of *Phytophthora rubi* isolates from raspberry (*Rubus idaeus*) in the western United States. Plant Dis. 98(12): 1702–1708. https://doi.org/10.1094/PDIS-11-13-1130-RE.

Stockton DG, Hesler SP, Wallingford AK, Leskey TC, McDermott L, Elsensohn JE, Riggs DIM, Pritts M, Loeb GM. 2020. Factors affecting the implementation of exclusion netting to control *Drosophila suzukii* on primocane raspberry. Crop Prot. 135:105191. https://doi.org/10.1016/j.cropro.2020.105191.

Sudars K, Namatēvs I, Judvaitis J, Balašs R, Ņikuļins A, Peter A, Strautiņa A, Kaufmane E, Kalniņa I. 2022. YOLOv5 deep neural network for quince and raspberry detection on RGB images, p 19–22. In: 2022 Workshop on Microwave Theory and Techniques in Wireless Communications (MTTW), Riga, Latvia. Institute of Electrical and Electronics Engineers. https://doi.org/10.1109/MTTW56973.2022.9942550.

Tanksley SD. 1993. Mapping polygenes. Annu Rev Genet. 27:205–233. https://doi.org/10.1146/annurev.ge.27.120193.001225.

Theiler-Hedtrich R, Baumann G. 1989. Elimination of *Apple mosaic virus* and *Raspberry bushy dwarf virus* from infected red raspberry (*Rubus idaeus* L.) by tissue culture. J Phytopathol. 127(3):193–199. https://doi.org/10.1111/j.1439-0434.1989.tb01129.x.

Thompson MM. 1997. Survey of chromosome numbers in *Rubus* (Rosaceae: Rosoideae). Ann Missouri Bot Gard. 84(1):128–164. https://doi.org/10.2307/2399958.

Toussaint V, Valois D, Dodier M, Faucher E, Déry C, Brzezinski R, Ruest L, Beaulieu C. 1997. Characterization of actinomycetes antagonistic to *Phytophthora fragariae* var. *rubi*, the causal of agent of raspberry root rot. Phytoprotection. 78(2):43–51. https://doi.org/10.7202/706118ar.

Trudgill DL, Brown DJF. 1992. The effect of crop rotation and chemical soil treatment on the growth of raspberry (*Rubus idaeus*) in soils with replant problems. J Hortic Sci. 67(4):

541–546. https://doi.org/10.1080/00221589.1992.11516281.

US Department of Agriculture Economic Research Service. 2023. Fruit and tree nuts yearbook tables: Berries. https://www.ers.usda.gov/data-products/fruit-and-tree-nuts-data/fruit-and-tree-nuts-yearbook-tables/#Berries. [accessed 5 May 2023]. [data set].

US Department of Agriculture National Agricultural Statistics Service. 2024. Quick stats. https://quickstats.nass.usda.gov/. [accessed 13 Feb 2024]. [data set].

US Environmental Protection Agency. 2008. *Fenamiphos facts*. https://archive.epa.gov/pesticides/reregistration/web/html/fenamiphos_ired_fs.html. [accessed 13 Jan 2024].

Valois D, Fayad K, Barasubiye T, Garon M, Déry C, Brzezinski R, Beaulieu C. 1996. Glucanolytuic actinomycetes antagonistic to *Phytophthora fragariae* var. *rubi,* the causal agent on raspberry root rot. Appl Environ Microbiol. 62(5):1630–1635. https://doi.org/10.1128/aem.62.5.1630-1635.1996.

VanBuren R, Bryant D, Bushakra JM, Vining KJ, Edger PP, Rowley ER, Priest HD, Michael TP, Lyons E, Filichkin SA, Dossett M, Finn CE, Bassil NV, Mockler TC. 2016. The genome of black raspberry (*Rubus occidentalis*). Plant J. 87(6):535–547. https://doi.org/10.1111/tpj.13215.

VanBuren R, Man Wai C, Colle M, Wang J, Sullivan S, Bushakra JM, Liachko I, Vining KJ, Dossett M, Finn CE, Jibran R, Chagné D, Childs K, Edger PP, Mockler TC, Bassil NV. 2018. A near complete, chromosome-scale assembly of the black raspberry (*Rubus occidentalis*) genome. Gigascience. 7(8):giy094. https://doi.org/10.1093/gigascience/giy094.

van Emden HF. 2007. Host-plant Resistance, p 447–468. In: van Emden HF, Harrington R (eds). Aphids as crop pests. CABI, Wallingford, UK.

Vrain TC, Daubeny HA. 1986. Relative resistance of red raspberry and related genotypes to the root lesion nematode. HortScience. 21(6):1435–1437. https://doi.org/10.21273/HORTSCI.21.6.1435.

Vrain TC, Daubeny HA, Hall JW, DeYoung RM, Anderson AK. 1994. Inheritance of resistance to root lesion nematode in red raspberry. HortScience. 29(11):1340–1341. https://doi.org/10.21273/HORTSCI.29.11.1340.

Vrain T, DeYoung R, Hall J, Freyman S. 1996. Cover crops resistant to root-lesion nematodes in raspberry. HortScience. 31(7):1195–1198. https://doi.org/10.21273/HORTSCI.31.7.1195.

Walker A-S, Gautier AL, Confais J, Martinho D, Viaud M, Le P Cheur P, Dupont J, Fournier E. 2011. *Botrytis pseudocinerea*, a new cryptic species casing gray mold in French vineyards in sympatry with *Botrytis cinerea*. Phytopathology. 101(12):14331–1445. https://doi.org/10.1094/PHYTO-04-11-0104.

Walters TW, Bolda M, Zasada IA. 2017. Alternatives to current fumigation practices in western states raspberry. Plant Health Progress. 18(2):104–111. https://doi.org/10.1094/PHP-RS-16-0068.

Wang L, Lei T, Han G, Yue J, Zhang X, Yang Q, Ruan H, Gu C, Zhang Q, Qian T, Zhang N, Qian W, Wang Q, Pang X, Shu Y, Gao L, Wang Y. 2021. The chromosome-scale reference genome of *Rubus chinigii* Hu provides insight into the biosynthetic pathway of hydrolysable tannins. Plant J. 107(5):1466–1477. https://doi.org/10.1111/tpj.15394.

Ward JA, Boone WE, Moore PP, Weber CA. 2012. Developing molecular markers for marker assisted selection for resistance to *Raspberry bushy dwarf virus* (RBDV) in red raspberry. Acta Hortic. 946:61–66. https://doi.org/10.17660/ActaHortic.2012.946.6.

Washington State Department of Agriculture. n. d. Washington Agriculture. https://agr.wa.gov/washington-agriculture. [accessed 3 June 2025].

Weber CA. 2003. Genetic diversity in black raspberry detected by RAPD markers. HortScience. 38(2):269–272. https://doi.org/10.21273/HORTSCI.38.2.269.

Weber C. 2013. Cultivar development and selection, p 55–72. In: Funt RC, Hall HK (eds). Raspberries. CABI, Wallingford, UK.

Weber CA, Pattison J, Samuelian S. 2008. Marker-assisted selection for resistance to root rot in red raspberry caused by *Phytophthora fragariae* var. *rubi*. Acta Hortic. 777:311–316. https://doi.org/10.17660/ActaHortic.2008.777.46.

Weiland JE, Benedict C, Zasada IA, Scagel CR, Beck BR, Davis A, Graham K, Peetz A, Martin RR, Dung JKS, Gaige AR, Thiessen L. 2018. Late-summer disease symptoms in western Washington red raspberry fields associated with co-occurrence of *Phytophthora rubi, Verticillium dahliae,* and *Pratylenchus penetrans*, but not *Raspberry bushy dwarf virus*. Plant Dis. 102(5):938–947. https://doi.org/10.1080/15538362.2013.748373.

Weiland JE, Scagel CF, Benedict C, Wasko DeVetter L, Beck BR. 2024. Fungicide sensitivity of *Phytophthora* isolates from the Washington red raspberry industry. Plant Dis. 108(7):2104–2110. https://doi.org/10.1094/PDIS-12-23-2641-RE.

Wight H, Zhou J, Li M, Hannenhali S, Mount SM, Liu Z. 2019. Draft genome assembly and annotation of red raspberry *Rubus idaeus*. BioRxiv. https://doi.org/10.1101/546135.

Wilcox WF. 1989. Identity, virulence, and isolation frequency of seven *Phytophthora* spp. causing root rot of raspberry in New York. Phytopathology. 79(1):93–101. https://doi.org/10.1094/Phyto-79-93.

Wilcox WF, Cooke DEL. 2017. Phytophthora root rot, p 52–56. In: Martin RR, Ellis MA, Williamson B, Williams RN (eds). Compendium of raspberry and blackberry diseases and pests (2nd ed). APS Press, St. Paul, MN, USA.

Wilcox WF, Pritts MP, Kelly MJ. 1999. Integrated control of Phytophthora root rot of red raspberry. Plant Dis. 83(12):1149–1154. https://doi.org/10.1094/PDIS.1999.83.12.1149.

Williams D, Britten A, McCallum S, Jones H, Aitkenhead M, Karley A, Loades K, Prashar A, Graham J. 2017. A method for automatic segmentation and splitting of hyperspectral images of raspberry plants collected in field conditions. Plant Methods. 13:74. https://doi.org/10.1186/s13007-017-0226-y.

Williams D, Hackett CA, Karley A, McCallum S, Smith K, Britten A, Graham J. 2021. Seeing the word for the trees: Hyperspectral imaging for high-throughput QTL detection in raspberry, a perennial crop species. Fruit Res. 1:7. https://doi.org/10.48130/FruRes-2021-0007.

Williams D, Karley A, Britten A, McCallum S, Graham J. 2023. Raspberry plant stress detection using hyperspectral imaging. Plant Direct. 7(3):e490. https://doi.org/10.1002/pld3.490.

Williamson B, Tudzynski B, Tudzynski P, Van Kan JAL. 2007. *Botrytis cinerea*: The cause of grey mold disease. Mol Plant Pathol. 8(5):561–580. https://doi.org/10.1111/j.1364-3703.2007.00417.x.

Willman MR, Bushakra JM, Bassil N, Finn CE, Dossett M, Perkins-Veazie P, Bradish CM, Fernandez GE, Weber CA, Scheerens JC, Dunlap J, Fresnedo-Ramírez J. 2022. Analysis of a multi-environment trial for black raspberry (*Rubus occidentalis* L.) quality traits. Genes (Basel). 13(3):418.

Wöhner T, Pinggera J, Fritzsche E, Peil A, Pinczinger D, Hanke M-D. 2021. Insights into the susceptibility of raspberries to *Drosophila suzukii* oviposition. J Appl Entomol. 145(3):182–190. https://doi.org/10.1111/jen.12839.

Worthington ML, Aryal R, Bassil NV, Mead D, Fernandez GE, Clark JR, Fernández-Fernández F, Finn CE, Hummer KE, Ashrafi H. 2020. Development of new genomic resources and tools for molecular breeding in blackberry. Acta Hortic. 1277:39–46. https://doi.org/10.17660/ActaHortic.2020.1277.6.

Yin YN, Kim YK, Xiao CL. 2012. Molecular characterization of pyraclostrobin resistance and structural diversity of the cytochrome *b* gene in *Botrytis cinerea* from apple. Phytopathology. 102(3):315–322. https://doi.org/10.1094/PHYTO-08-11-0234.

Zasada IA, Halbrendt JM, Kokalis-Burelle N, LaMondia J, McKenry MV, Noling JW. 2010. Managing nematodes without methyl bromide. Annu Rev Phytopathol. 48:311–328. https://doi.org/10.1146/annurev-phyto-073009-114425.

Zasada IA, Meyer SLF, Morra MJ. 2009. Brassicaceous seed meals as soil amendments to suppress the plant-parasitic nematodes *Pratylenchus penetrans* and *Meloidogyne incognita*. J Nematol. 41(3):221–227.

Zasada IA, Moore PP. 2014. Host status of *Rubus* species and hybrids for the root lesion nematode, *Pratylenchus penetrans*. HortScience. 49(9):1128–1131. https://doi.org/10.21273/HORTSCI.49.9.1128.

Zasada IA, Weiland JE, Han Z, Walters TW, Moore P. 2015. Impact of *Pratylenchus penetrans* on establishment of red raspberry. Plant Dis. 99(7):939–946. https://doi.org/10.1094/PDIS-09-14-0980-RE.

Zeller SM. 1936. Verticillium wilt of cane fruits. Agric Exp Stn Bull 344.

Zhang H, Miles C, Ghimire S, Benedict C, Zasada I, DeVetter L. 2019. Polyethylene and biodegradable plastic mulches improve growth, yield, and weed management in floricane red raspberry. Sci Hortic. 250:371–379. https://doi.org/10.1016/j.scienta.2019.02.067.

Zhang X, Xie F, Lv B, Zhao P, Ma X. 2016. Suspension array for multiplex detection of eight fungicide resistance-related alleles in *Botrytis cinerea*. Front Microbiol. 7:1482–1491. https://doi.org/10.3389/fmicb.2016.01482.

Ziegler A, Mayo MA, Murant AF. 1993. Proposed classification of the bipartite-genomed raspberry bushy dwarf idaeovirus, with tripartite-genomed viruses in the family Bromoviridae. Arch Virol. 131(3–4):483–488. https://doi.org/10.1007/BF01378649.

Ziegler A, Natsuaki T, Mayo MA, Jolly CA, Murant AF. 1992. The nucleotide sequence of RNA-1 of *Raspberry bushy dwarf virus*. J Gen Virol. 73:3213–3218. https://doi.org/10.1099/0022-1317-73-12-3213.

Zhu C, Gore M, Buckler ES, Yu J. 2008. Status and prospects of association mapping in plants. Plant Genome. 1(1):5–20. https://doi.org/10.3835/plantgenome2008.02.0089.