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REVIEW

Horticulture of *Ribes*

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Summary

The genus *Ribes* L., known as currants and gooseberries, contains more than 150 diverse species indigenous throughout the northern hemisphere and along the Rocky Mountain, Sierra Nevada and Sierra Madres in North America through mountain ranges of Central America to the Andes in South America. Beginning in the 1400s, four main crop types, black currants (*Ribes*, subgenus: *Ribes*, section: *Botrycarpum*), red and white currants (*Ribes*, subgenus: *Ribes*, section: *Ribes*) and gooseberries (*Ribes*, subgenus: *Grossularia*) were domesticated from European species. American and Eurasian species were selected and combined into the germplasm base of European and American breeding programmes in the 1900s. Black currants (*R. nigrum* and hybrids) are a major economic crop in many European countries but are minor in North America, although they can be produced successfully in the northern states and southern portion of the Canadian provinces. *Ribes* plants can be hosts for white pine blister rust, caused by *Cronartium ribicola*. This disease was introduced from Asia through Europe into North America ca. 1900. Restrictions were imposed on currants and gooseberries in the United States when the rust was observed on this continent. Although some states have recently repealed these restrictions, by 2009, 12 states continue to have 40-year-old laws prohibiting or restricting *Ribes* cultivation. The purpose of this paper is to describe the cultivation of currants and gooseberries and their interaction with rust. *Ribes* production has a potentially great economic value in American, niche markets that could help sustain small-acreage, berry farmers.

1 Introduction

Currants and gooseberries, genus *Ribes* L., family Grossularia L., include more than 150 described species (see Geils et al. 2010; : Fig. 2). Most of the commercial production of *Ribes* fruits occurs in northern Europe. The black currants are the major crop and their juice the major product. *Ribes* products include jams, jellies, liqueurs (crème de cassis), colourants for conversion of white wines to rosé, teas, additives to dairy products, and extracts for nutritional supplements (Brennan 1996). During the past 20 years, world currant production has almost doubled from 550 to more than 1017 t (Food and Agriculture Organization 2007). However, the market must expand globally if increased production is to be supported. For the past decade, however, surplus global production has depressed market price.

In the early 1900s, more than 2900 ha of currants and gooseberries were in commercial production in North America. In 1919, the United States current crop was worth more than $1.4 million (Hedrick 1925). By 1929, only about 500 ha of gooseberries were reported. As of 2007, the North American production of *Ribes* has been insufficient to be annually reported by the Food and Agriculture Organization of the United Nations. Commercial area in North America is small and scattered but is increasing. Small-acreage farmers throughout the Pacific Northwest and Northeastern United States and Canada are

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diversifying their crop production; and some are planting areas of usually less than 2–4 ha to *Ribes.*

2 Biology

2.1 Classification

Ribes was previously classified in the family Saxifragaceae, but recent taxonomic treatments place the genus into Grossulariaceae based on presence of wholly inferior ovaries, totally syncarpous gynoecium, and fleshy fruits (Cronquist 1981; Sinnott 1985). Previous, botanical references defined separate genera for currants and gooseberries (Coville and Britton 1908; Berger 1924; Komarov 1971). Most taxonomists now recognize a single genus (Janczewski 1907; Sinnott 1985). That gooseberry and currant species are able to hybridize supports the single-genus concept (Keep 1962).

The genus has five subgenera: (1) *Berisia*, European dioecious plants; (2) *Grossularia*, gooseberries; (3) *Grossularioides*, thorny currants; (4) *Parilla*, South American natives and (5) *Ribes*, currants. This paper will focus on the subgenera *Grossularia* and *Ribes* which contain the cultivated *Ribes* crops of economic interest. The subgenus *Grossularia* includes two sections, *Grossularia*, true gooseberries, and *Robsonia*, fuchsia-like flowered gooseberries. Gooseberry fruit colour can ripen green, yellow, red, purple or black depending on the genotype. The subgenus *Ribes* includes eight sections, four of which are of importance to cultivated forms: (1) *Botrycarpum* (formerly *Coreosma*), the black currants, the most economically important section; (2) *Calobotrya*, ornamental currants; (3) *Ribes*, red and white currants and (4) *Symphocalyx*, golden-flowered currants with black fruits.

2.2 Centres of diversity

Wild *Ribes* species are indigenous, circumpolar, boreal, and in the mountains of North, Central and South America. The primary centres for the ancestors of the cultivated black and red currants are northern Europe, Scandinavia and the Russian Federation (Rehder 1986; Jennings et al. 1987). Ancestors for the cultivated gooseberry originated in Europe and from western North America, a region rich in gooseberry species diversity. Several species of black currants with sessile, yellow glands originated in South American highlands. Ornamental and golden currants are native to North and Central America. The principal evolutionary trend in these groups appears to be biogeographical (Sinnott 1985). Messinger et al. (1999) suggested two possible, not mutually exclusive, evolutionary scenarios for *Ribes*—long periods of stasis interrupted by sudden radiation of species and gene flow from hybridization as a process of diversification.

2.3 Domestication

In Europe, red currants have been gathered and grown since the 1400s for food and medicines. In 1887, Sturtevant (republished in Hedrick 1919) and Hedrick (1925) compiled histories of currant domestication. Red currants were probably first cultivated in the Netherlands, Denmark and the coastal plains surrounding the Baltic (Hedrick 1925). Selected plants of these crops were imported to England and France. By the 1500s, the cultivation and consumption of red currants were well documented. Phillips (1831) described red and white currants as popular for desserts and proclaimed them to be soothing to the stomach. White currants were used for table wines by the 1800s.

In the early and mid-1900s, the discovery that black currant fruits had a high content of vitamin C (ascorbic acid) promoted crop development as a healthful drink throughout Europe, where citrus could not be grown and was expensive to import. Cultivated black currant fruit contain from 50 to 250 mg vitamin C per 100 g fresh weight of fruit, and some wild species contain up to 800 mg per 100 g fresh weight. Recently, nutritionists have emphasized the importance of antioxidants to reduce cancer, heart disease and other health concerns. Black currants contain high concentrations of total phenolics, anthocyanins, and are high in antioxidant capacity (Moyer et al. 2002a,b). The antioxidant levels of black currants occur in the high range of blueberries, blackberries and black raspberries, which are higher than other red-coloured fruits, such as strawberries and red raspberries, which are in turn much higher than vegetables (Wang et al. 1997).

2.4 Cultivated *Ribes* in North America

European currants (probably reds) were introduced into Massachusetts with the first English colonists (Sturtevant cited in Hedrick 1919). A memorandum by the Massachusetts Company, 16 March 1629, stated that they were providing for the interests of the colony in the New World: 'To provide to send for New England, vyne planters, stones of all sorts of fruites ...', and continues by specifically mentioning 'currant plants' among many fruit crops on their shipping list. Sturtevant further related that, 'In these early days the exchange of plants might be expected to be in their most condensed state, that is seeds...as we examine the records of the next century (1600s) we shall find additional records of improved varieties just as if the advice of growing seedlings had been followed, and the better forms gained had been propagated by cuttings'. White and black currant plants were probably introduced along with the reds.

Early nursery catalogues in North America document multiple currant plant offerings. In 1770, Prince Nurseries of Flushing, New York, offered red, white and black currants. By the mid- 1850s, 25 different cultivars of European currants were described and available for purchase in North America. Cultivated European currants were available for purchase and were widely planted throughout the North American colonies before the white pine blister rust pathogen (*Cronartium ribicola* J. C. Fisch. in Rabh.) was imported from Asia into Europe. Hedrick (1925) described 185 currant cultivars, 109 of which were selected or developed in North America.

Fruits of the native, western prairie gooseberry (*R. oxyacanthoides* L.) were well used by the Indians of Colorado, Arizona, Oregon, California, and Utah long before Europeans reached the North America (Hedrick 1919). In the mid-1600s, the imported European gooseberries proved to be susceptible to powdery mildew (*Sphaerotheca*) and did not grow well. Selections of native American species were grown and crossed with European plants to produce resistant gooseberries for commercial production (Hedrick 1919).

White pine blister rust was introduced from Europe to North American on many occasions in the several decades around 1900 (Geils et al. 2010). Although there was some concern that the fungus was introduced on diseased *Ribes*, it was introduced on rust-infected white pine seedlings imported from Europe. The principal threat attributed to *Ribes* at this time was the high inoculum potential seen on *Ribes nigrum* L., the cultivated European black current (Spaulding 1922b).

By 1935, A. W. Hunter, a Canadian fruit breeder in Ontario, Canada, had developed rust resistant black currants incorporating the rust-resistant *Cr* gene from the Siberian species *R. ussuriense* Jancz., that he had obtained from a botanical garden in Poland. The black currant cultivars 'Crusader', 'Coronet' and 'Consort' were released by Hunter (1950, 1955). Unfortunately, these three cultivars, while not hosting inoculum of white pine blister rust, were highly susceptible to powdery mildew and produced fruit of inferior quality. These cultivars were never greatly desired for commercial production. In 1981, Pal Tamas, a Hungarian-borne Swedish breeder, released the black currant 'Titania', which has the *Cr* gene, plus powdery mildew resistance (from genes derived from American gooseberry species), and improved yield. However, the quality of 'Titania' juice is not accepted against other European commercial cultivars. Growers who have planted this resistant black currant have removed it from their blocks and replanted with black currants with higher quality fruit (D. Peacock, personal communication). The growth habit of 'Titania' is too spreading for mechanical harvesters. European and American *Ribes* breeders are collaborating to continue their efforts to develop black currant cultivars with resistance or immunity to white pine blister rust, improved fruit quality and higher yield (R. Brennan, personal communication). Some Polish cultivars have rust resistance but are not yet available in domestic American nurseries. Within a few years, additional cultivars with high quality fruit and resistance to rust and mildew should be released.

2.5 Environmental limitations

Currants grow and are adapted to temperate climates. They are noted for their cold hardiness. Most species can survive mid-winter temperatures of −40°C or lower (Harmat et al. 1990). The cultivated black and red currants perform best in climates with cold winters and moderate rather than hot summers. *Ribes* have two chilling requirements—buds require about 1000 h of chilling to break dormancy and blooming requires 160 to 200 growing-degree-days (base of 5°C). The time to fruiting is relatively short, 120 to 140 frost-free days (Harmat et al. 1990). Plants perform best on deep, organic, well-drained soils with good water-holding capacity. The soil pH should be between 5.5 and 7.0. Dale (2000) suggested that the limit for production at high latitudes could reasonably be identified as 1200 growing-day-degrees above 5°C and the limit at low latitudes would reasonably be 1200 h below 7°C.

3 Genetics

While *Ribes* has great diversity in plant morphology and characteristics, the chromosomes are small, 1.5–2.5 μm (Darlington 1929), and uniform (Sinnott 1985). Mitotic and meiotic processes are regular (Zielinski 1953). *Ribes* species are diploid and have a base chromosome number of $2x = 2n = 16$.

Ribes flowers occur in racemes. Red and white currants tend to have longer racemes than do black currants. Gooseberries have the shortest racemes, with flowers borne singly or with two per raceme. Bees and other insects are the main pollinators. Most black currant pollen is released from the anthers between 2:00 and 6:00 PM; so, most pollination occurs during the day (Baldini and Pisani 1961). Self-incompatibility predominates among wild *Ribes* (Brennan 1996). Only two black currant cultivars have been reported with complete self-sterility, although highly reduced self-fertility is more common. Fernqvist (1961) observed that black currants had little or no difference in fruit-set after self-pollination, cross-pollination, or open-pollination. In contrast, Baldini and Pisani (1961) observed that fruit-set was considerably increased by cross-pollination; however, differences occurred with different pollen parents. Commercial fields of *Ribes* are planted with pollinizer cultivars to ensure and enhance fruit set (Barney and Hummer 2005). Natural apomixis and parthenocarpy are rare in the genus (Brennan 1996). Application of indoleacetic acid, indolebutyric acid and gibberillic acid (GA3) can induce apomixis; and GA3 can induce parthenocarpy in black currants, red currants and other species (Zatykó 1962).

A diverse assortment of wild species is being incorporated into breeding programmes. Genetic solutions to physiological and resistance challenges are being sought. The success of inter-specific hybridization depends on whether the planned cross is inter- or intra-sectional (Brennan 1996). The process for intra-sectional hybridization is as straightforward as conventional intra-specific crosses and can produce potentially commercially acceptable seedlings in the first backcross stage. The processes for inter-sectional and intersubgeneric crosses are more involved. Usually, sterile diploids are produced from which fertile allotetrapoloids can be obtained. Then, complex processes involving several generations of breeding using induced polyploidy with backcrossing and selections may produce the desired genotype.

Brennan (1996) listed 21 genes described in the literature. These genes include resistance to fungal and insect pests such as mildew and blister rust and plant characteristics for fruit colour, male sterility, thorniness and leafing-out season. DNA marker patterns using randomly amplified polymorphic DNA, amplified fragment length polymorphisms, and inter-simple sequence repeats (ISSR) are being developed for gene mapping and identification of specific genes (Lanham and Brennan 1999; Brennan et al. 2002b; and see Richardson et al. 2010).

The major breeding efforts have occurred in the United Kingdom, Norway, Sweden, Finland, Russia, Poland, Czech Republic, Ukraine, Lithuania, Canada, and New Zealand. Breeding efforts in the United States and Canada are evaluating crosses from European programmes (Rousseau et al. 2002). Selection objectives vary by region. In Europe, emphasis is for high fruit-quality, in particular, for high levels of ascorbic acid (Brennan and Gordon 2002). Major agronomic objectives include tolerance to spring frosts, pests and diseases. For pests and diseases, the European focus is for mite and virus disease resistance; but the North American interest is for resistance to mildew and *Cronartium ribicola* (the *Cr* gene). Crosses have been made to incorporate the *Cr* gene into selections with high-quality and high-yielding fruit on plants of good structure. New releases for North America are available or expected. Cultivars homozygous for *Cr* are requiring additional work (R. Brennan and J. Luby, personal communication). In New Zealand, the main objective is to incorporate gall mite resistance into cultivars with reduced chilling requirements.

4 Pests and diseases

Ribes production is beset by different diseases and pests on different continents. In Europe and New Zealand, the key pests are black currant reversion virus (BCRV), vectored by the black currant gall mite (*Cecidophyopsis ribis* Westw.). This disease–pest complex is devastating to commercial black currant production. Incidence higher than 5% make the crop unprofitable. Neither the BCRV nor the black currant gall mite is present in the United States (Amrine 1992) or Canada (A. Dale, personal observation); so, these American countries have quarantines prohibiting *Ribes* to enter without being tested for these pests (Animal and Plant Health Inspection Service 2000). Other viruses and virus-like diseases also occur in *Ribes* (Converse 1987). Aphids vector gooseberry vein banding and cucumber mosaic; nematodes vector arabis mosaic virus and several other nepoviruses.

In North America, the most serious diseases of *Ribes* include powdery mildew, white pine blister rust and *Botryosphaeria* dieback (*Botryosphaeria ribis*). A *Puccinia* rust can affect *Ribes* growing in wet areas in the early spring. Pests include the currant aphid (*Cryptomyzus ribis* L.), the currant cane borer (*Synanthedon tipuliformis* Cl.), the currant fruit fly (i.e. the gooseberry maggot, *Epochra canadensis*), the gooseberry mite (*Cesidophyopsis grossularae* Coll.) and the gooseberry sawfly (*Nematus ribesii* Scop.).

4.1 Powdery mildew

Powdery mildew over-winters on currant twigs and infects shoots, leaves and berries during the spring and summer. The disease appears as white powdery growths on the surface of leaves and young green shoots. Affected leaves develop scorch symptoms, become deformed and dry out. During hot weather, damaged leaves may fall. On berries, mildew produces a dark brown, felt-like coating that renders the fruit unmarketable. Infected plants are often stunted, and severely affected plants can be killed. The best management strategy is to plant resistant cultivars, although mineral oil sprays, soaps and fungicides can provide control (Hummer and Picton 2001; Picton and Hummer 2003a,b). A spectrum of genetic resistance is present in the black currant genome, ranging from highly susceptible to highly resistant. Red and white currants show foliar symptoms, but fruit symptoms can occur in areas of high infection.

4.2 White pine blister rust

Aeciospores of *C. ribicola* are produced on pines and may travel 1000s of kilometres to infect currants (Frank et al. 2008). Susceptible European black currants produce more uredinia and thus more inoculum than is generated from the less susceptible red or white currants. However, several black currant cultivars have a *Cr* gene which provides a high level of resistance or immunity. Uredinia do not form on the leaves of these genotypes.

Urediniospores are produced in uredinia on the underside of infected currant leaves. Throughout the summer, urediniospores spread the rust within an infected plant and to other nearby plants. Severely infected plants may lose their leaves prematurely. At the end of the summer, brown, telia-bearing teliospores form on the underside side of the currant leaves. Teliospores germinate in place to produce basidiospores capable of infecting susceptible pines. Because basidiospores are relatively delicate (see Geils et al. 2010), spread from current to pine is usually restricted to 10s or 100s of metres or rarely to several kilometres

Foliar applications of highly refined mineral oils can reduce white pine blister rust in susceptible black and red currants (Picton and Hummer 2003a). Foliar application of soaps may also reduce the rust (K. E. Hummer, personal observation).

4.3 Botryosphaeria

Botryosphaeria species are known to produce cankers and dieback in several woody hosts. *Botryosphaeria ribis* causes dieback of stems in susceptible currants and gooseberries. This disease is more severe after intermittent frosts in the early spring have damaged terminal branch tips. The fungus enters through damaged branch tips and causes severe dieback. *Botrytis cinerea* Pers. commonly infects branches after they have been killed by *Botryosphaeria*.

4.4 Botrytis

The gray mold fungus, *Botrytis cinerea,* causes several problems in association with *Botryosphaeria* on susceptible *Ribes*—dieback of shoots in the spring, premature fruit drop and fruit rot. Many golden currants (section *Symphocalyx*) are particularly susceptible to stem dieback. In addition, many cultivated black and red currants are subject to ‘run-off’ or premature fruit drop. Susceptibility to run-off is genotype dependant and can be selected against in breeding programmes (Brennan 1996).

4.5 Puccinia rust

Cluster cup rust, *Puccinia caricina* D.C., produces yellow spots on leaves, flowers and developing fruits of *Ribes* in April and May. The affected *Ribes* usually grow in low lying areas such as swamps with sedges (*Carex*). For *P. caricina, Ribes* are the aecial host and sedges are the uredinial host. This disease can significantly reduce the yield of black fruited currants and be significant in the midwestern and northern prairie states.

4.6 Cane borer

Currant cane borer is native to Europe but was introduced into North American in the 1890s and has since spread across the continent (James et al. 2001). This insect infests black, red and white currants. In August, the female lays eggs in nodes of 1- to 5-year wood. During the winter, the larvae burrow into the stem and feed in the centre of the canes, blackening the inside. In May, the larvae pupate and emerge as adults to begin the cycle over again. During the summer, as the *Ribes* branches are laden with heavy ripening fruit, the canes lodge in the rows. Previously infected canes can no longer support upright branches including the fruit weight. Most *Ribes* cultivars are infested by cane borers (Hummer and Sabitov 2003). Pheromone mating disruption techniques are under research as control technique. Mating disruption is optimal where infestation levels are less than 0.6 larvae per cane during the dormant season (James et al. 2001).

4.7 Aphids

Over 12 aphid species, including *Hyperomyzus lactucae* L., *Hyperomyzus pallidus* (H.R.L.), *Cryptomyzus ribis* L., *Nasonovia ribisnigri* Mosley and *Aphis* spp., infest currant species (Brennan 1996). These pests cause leaf blistering, reddening, discolouration and stem deformation in black, red and white currants. The amount of leaf damage ranges from cosmetic to severe. Aphids also cause economically significant damage as vectors of viruses. Pesticide or soap treatments before flowering and after harvest can limit the damage caused by these pests.

4.8 Sawfly

The caterpillars of the gooseberry sawfly feed voraciously on gooseberry leaves in early summer (Hummer and Postman 2004). They sometimes defoliate a complete bush, leaving only the midrib and main veins, and reducing fruit yield. At least six *Calobotrya* species, including *R. sanguineum* Pursh., *R. menziesii* Pursh., *R. roezlii* Reg., appear to be resistant (Brennan 1996).

5 Culture

Harmat et al. (1990), Audette and Lareau (1996) and Barney and Hummer (2005) describe in detail the culture of *Ribes*. The following section is based on their descriptions unless otherwise stated.

5.1 Propagation

Ribes are easily propagated from hardwood stem cuttings, except for European gooseberries. Cuttings are usually about 20 cm long for black currants and 30 cm long for red currants and gooseberries. The latter are ‘layered’ by bending the shoots to the ground, covering them with soil, and allowing roots to develop. Hardwood cuttings are grown for 1 or 2 years to produce plants that are dug and replanted in fruiting fields. The lower buds of red currant and gooseberry cuttings are removed to develop a short trunk or ‘leg’. Growers buy either hardwood cuttings or plants depending on their view of economic prospects. Hardwood cuttings cost less but take longer to come into full production than plants. Cuttings can be rooted in the northern hemisphere from September through April. Other types of propagation include softwood cuttings and tissue culture. Softwood cuttings can be taken during the growing season and will root successfully if they do not dry out. Tissue culture (Wainwright and Flegmann 1986) is expensive and used primarily to increase a new cultivar or to eradicate viruses.

5.2 Fruit growing

Black, red and white currants and gooseberries have several cultural practises in common. Plantations achieve maximum yields after 3–5 years, depending on the type of propagation material. Plants are routinely fertilized with nitrogen, phosphorus and potassium and are irrigated to maximize production. Integrated pest management programmes are used to control the major pests and diseases. Large plantations are not tilled, and selective herbicides are used to control weeds.

5.2.1 Black currants

Blocks of single cultivars are planted in rows with 0.75–1.5 m between plants and 2–3.5 m between rows. Plantations designed for mechanical harvesting are planted closer within and wider between rows than hand-harvested plantations. Plants annually produce new shoots from the crown. Mature plants are pruned to remove 3-year-old wood because most fruit is harvested from 1-year-old wood. In hand-harvested plantations, pruning requires many hours of manual labour. Most large plantations are now harvested mechanically to avoid expensive, hand labour. For mechanical harvesting, cultivars of compact growth are planted; bushes are mechanically pruned into hedgerows and small-bush harvesters are used (Dale et al. 1994). Ethephon is used in northern China to increase simultaneous ripening and improve hand labour efficiency (Zhang et al. 2002).

5.2.2 Red and white currants and gooseberries

These crops are planted in blocks with plants 1–1.25 m apart in rows and 2.4–2.7 m between rows. Plants can be left as bushes, grown on a short 'leg' or trained into a fan-shaped bush supported by trellising. The bushes produce fruit on short spurs from 2- or 3-year-old wood. The plant is pruned to maintain a balance between new vegetative growth and fruiting wood. Fruit is harvested mainly by hand for the fresh market. In northern Europe, the plantations are covered with a rain shelter to keep the plants dry and extend the harvest period from a few weeks to several months.

6 Commercial prospects

World production of currants and gooseberries has increased during the past several years to 1017 t in 2005 (Food and Agriculture Organization 2007). More than 99% of the production is European; the Russian Federation, Germany and Poland contribute >80% of the total. Outside Europe, only New Zealand produces significant amounts. Production figures are unavailable for China, but black currants are an important small fruit crop the northern provinces of Heilongjiang, Jilin, Liaoning, Xinjiang and Inner Mongolia (Zhang et al. 2002). Production in Canada and the United States is small and estimated at 60 to 120 tons per year.

Ribes fruit is used mainly as processed products, but red and white currants and gooseberries are edible as a fresh dessert. Processed products include juice, jams and preserves, pie fillings, dessert toppings, yogurt, ice cream, mineral waters, teas, liqueurs, candies and perfumes. The seeds have commercial potential as a herbal concentrate because of their gamma-linolenic acid content. About 80% of the black currant crop is extracted for a juice which is extremely high in vitamin C, four times higher than that in oranges, *Citrus* *sinensis* (L.) Osbeck., and 50 times higher than in apples, *Malus domestica* Borkh. (Westwood 1993).

Dale (2000) reviewed the potential for commercial *Ribes* production in North America. He concluded that currants and gooseberries could be grown throughout most of North America. For large-scale production, markets would needed processed products. Producers have been scattered, small-scale operations; they usually service niche markets such as 'pick-your-own' farms. Many value-added, imported products are available in Canadian retail markets. Dale (2000) concluded that the major market required for expansion would be for juice production. If suitable markets are developed, North America could support a *Ribes* industry similar in size to that of Poland, one of the largest consumer countries for *Ribes* products in the world.

7 Information needs

Several questions remain regarding *Ribes* in the white pine blister rust life cycle. Research needs to address the following concerns.

7.1 *Cronartium ribicola–Ribes* interaction

7.1.1 Basidiospore production and dispersal

Of the many stages of *C. ribicola* on *Ribes*, only basidiospores infect white pines. We need to know what factors induce them to form, how they develop and what their dispersal mechanisms are. Although urediniospores are produced, the cycle from *Ribes* to pine could be broken before the basidiospores are formed through cultural control measures, such as a foliar oil spray, or through reducing production of probasidia.

7.1.2 Basidiospore and teliospore survival

Several studies have shown that *C. ribicola* basidiospores travel fairly short distances, but this needs further quantification. Because the morphology of the basidiospore suggests that it is not long-lived and because infected *Ribes* leaves senesce early and drop to the ground, the period of basidiospore release can be short. This production period needs to be quantified under various environments, and the likelihood of over-wintering re-examined. The survival of teliospores also needs to be investigated.

7.1.3 Ribes *infectivity by aeciospores*

Because *R. nigrum* is highly susceptible to infection by aeciospores, commercial fields could be a 'target' for long-distance infection with wind-blown aeciospores. This concept needs to be examined and statistical models developed to define how frequently this occurs.

7.2 Genecology

Foresters have expressed concern that highly susceptible genes from European cultivated currants could escape into native plant systems (see Zambino 2010). Evidence from the United Kingdom and Europe has indicated that very few seedlings of cultivated *R. nigrum* escape from large commercial plantations to the surrounding woods. The genes could move by pollen to cross with wild species and by seed through bird transmission. Hybrids between species of different *Ribes* sections have a low viability; but where native American species, such as *R. hudsonianum* or *R. americanum,* are present, crosses with *R. nigrum* could occur. North American studies are needed to estimate the movement of susceptible genes into the native species.

To determine if small plantings of cultivated European black currants could increase the susceptibility of the native *Ribes* population in North America, several studies need to be performed. First, the overall susceptibility of native, American *Ribes* must be determined. Then, the fitness of the European black currant to establish in North America must be estimated; and a comparison performed to the native susceptibility.

Cultivated *Ribes* could have escaped into North American forests through abandoned settlements from a century ago. This possibility could be explored if wooded areas which were first settled by colonists were surveyed for escaped *R. nigrum*, e.g. Connecticut and Geneva, New York; Vineland, Ontario; and Backus Woods, the largest existing tract of Carolinian Forest in Canada.

7.3 Genetic studies of resistance in *Ribes*

In the section *Botrycarpum* (black currants), at least one dominant gene for resistance to *C. ribicola*, *Cr*, has been identified. Other genetic resistance mechanisms are found in other sections; so, the gene pool in North America needs to be surveyed to find what alternative resistance mechanisms exist. These would enable broader resistance systems to be developed in cultivated currants.

Concern has been expressed about the stability of the *Cr* gene. Cultivars containing this gene were first developed in the 1930s (Hunter 1955), and this resistance has not been broken as of 2007. Although a differential responses to rust ecotypes have not been observed in *Ribes* cultivars with the *Cr* gene (Zambino 2000), monitoring should continue for a possible breakdown of resistance.

7.4 Cultivation

Although white pine blister rust is considered a serious disease on black currants, no studies have been carried out to quantify the impacts of *C. ribicola* on the commercial yields of the plantations in North America. In some cases, rust may be controlled indirectly because of other farming cultural practises, such as oil sprays applied for mildew or soaps applied for aphid control. *Ribes* plants are usually moved within North America as dormant leafless cuttings or plants. This most likely does not contribute to the spread of rust, because natural infection of *Ribes* occurs within leaves, not systemically within the plant. *Ribes* propagules need to be tested for rust dispersal.

8 Conclusion

The genus *Ribes* contains many species that are grown commercially for fruit production, particularly in Europe. These species are highly variable; and, while many of the cultivars are susceptible to *C. ribicola*, genetic resistance exists. The *Cr* gene is known, but other mechanisms exist that could be exploited in future breeding efforts.

North America is a centre of diversity for *Ribes*; so, many of the genes necessary for modern breeding efforts can be found there. This variability will remain largely unexploited until a horticultural industry reaches a critical mass to demand further research.

From a horticultural perspective, a North American *Ribes* industry has commercial potential. *Ribes* fruit contains health-promoting, nutraceutical compounds. Success of these crops would require the development of suitable, country markets. Rust resistant cultivars and disease control measures could permit currant and gooseberry fruit production without increasing white pine blister rust incidence in pines.

Much of the white pine blister rust life cycle is known, but gaps concerning the interaction between blister rust, white pine and *Ribes* could be further examined. A continued dialogue between horticulturists, foresters and pathologists can lead to a balance of the needs of the international, national and regional lumber and horticulture industries.

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