DIVERSITY OF ADAPTATION, AGRONOMIC POTENTIAL AND FRUIT QUALITY OF

LONICERA CAERULEA L.

A Thesis Submitted to the College of
Graduate and Postdoctoral Studies
In Partial Fulfillment of the Requirements
For the Degree of Doctor of Philosophy
In the Department of Plant Sciences
University of Saskatchewan
Saskatoon
Saskatchewan

By

Eric Gerbrandt

PERMISSION TO USE

In presenting this thesis/dissertation in partial fulfillment of the requirements for a Postgraduate degree from the University of Saskatchewan, I agree that the Libraries of this University may make it freely available for inspection. I further agree that permission for copying of this thesis/dissertation in any manner, in whole or in part, for scholarly purposes may be granted by the professor or professors who supervised my thesis/dissertation work or, in their absence, by the Head of the Department or the Dean of the College in which my thesis work was done. It is understood that any copying or publication or use of this thesis/dissertation or parts thereof for financial gain shall not be allowed without my written permission. It is also understood that due recognition shall be given to me and to the University of Saskatchewan in any scholarly use which may be made of any material in my thesis/dissertation.

Requests for permission to copy or to make other uses of materials in this thesis/dissertation in whole or part should be addressed to:

> Head of the Department of Plant Sciences
> 51 Campus Drive,
> University of Saskatchewan
> Saskatoon,
> Saskatchewan,
> Canada,
> S7N 5A8

ABSTRACT

Blue honeysuckle (*Lonicera caerulea* L.) is a novel perennial fruit crop with northern climatic adaptation. Its extreme winter hardiness, early-season fruiting, high antioxidant content and unique flavour profiles have brought it attention as a niche-crop. Breeding for temperate regions that are suited to large-scale horticultural production is relatively recent. Barriers to large-scale commercial production include a low chilling requirement, resulting in early bud break, winter damage and poor pollination in temperate climates; modest yields, irregular fruit shapes and agronomic traits that limit harvestability and marketability; and a low sugar to acid ratio with questionable claims of potential human health benefits due to widely varying reports of antioxidant activity.

With the long-term objective of expanding the commercial potential of the crop, germplasm evaluation in a major fruit production region, the Fraser Valley, British Columbia, Canada, assessed phenological adaptation to a temperate climate, fruit morphological traits associated with agronomic potential and fruit biochemical characteristics related to fruit quality and nutritional content. Direct comparison of phenology and biochemistry to three globally important commercial crops, highbush blueberry, red raspberry and June-bearing strawberry, were conducted over two years with biological replication across multiples sites. Genetic diversity was characterized between three foundation germplasm groups, and the potential to make genetic progress was assessed in three improved groups. Physiological and genetic complexity was elucidated for economically important phenotypic responses to the target environment through comparison of improved germplasm with their parental foundation genotypes.

This work demonstrates that there is sufficient variation in phenology to permit crop adaptation to a temperate climate, which will make it possible to broaden the range of the crop into major fruit production regions. It shows that diversity in fruit morphological features can be used to breed for large-scale commercial agronomic potential. It characterizes fruit biochemical diversity, signifying commercially marketable fruit quality paired with high nutritional content related to potential human health benefits. This fundamental information on crop genetic resources and the genetic control of important traits will inform breeding strategies that will transform blue honeysuckle from a niche to commercial crop.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

xvi

xviii

LIST OF APPENDICES

LIST OF ABBREVIATIONS

ABTS	:	2,2'-asino-bis(3-ethylbenzothiazoline-6-sulphonic acid)
ABTS+	:	ABTS radical
AA	:	Ascorbic acid
AAE:	:	Ascorbic acid equivalents
AAHP	:	2,2'-Azobis(2-methylproprionamidine)dihydrochloride
AO	:	Antioxidant
AOA	:	Antioxidant activity
BC	:	British Columbia
Cfb	:	Temperate oceanic climate
Csb	:	Warm-summer Mediterranean climate
Dfa	:	Hot-summer humid continental climate
Dfb	:	Warm-summer humid continental climate
Dfc	:	Subarctic climate
DL	:	Day-length
DM	:	Percent dry weight
DMSO	:	Dimethyl sulfoxide
DNA	:	Deoxyribonucleic acid
DPPH	:	di(phenyl)-(2,4,6-trinitrophenyl)iminoazanium
Dsc	:	Dry-summer subarctic climate
DW	:	Dry weight
Dwb	:	Monsoon-influenced warm-summer humid continental climate
Dwc	:	Monsoon-influenced subarctic climate
ET	:	Electron transfer
FC	:	Folin-Ciocalteau
FQ	:	Fruit quality
FRAP	:	Ferric reducing antioxidant potential
FW	:	Fresh weight
GA	:	Gallic acid
GAE	:	Gallic acid equivalents
HAT	:	Hydrogen atom transfer

HPLC	:	High-pressure liquid chromatography
H^2	:	Broad-sense heritability
h^2	:	Narrow-sense heritability
KGCC	:	Köppen-Geiger climate classification
NCGR	:	National Clonal Germplasm Repository
ORAC	:	Oxygen radical antioxidant capacity
OP	:	Open pollination/pollinated
SE	:	Standard error
SI	:	Selection index
SO	:	Superoxide
SOD	:	Superoxide dismutase
pH	:	Potential of hydrogen
PSM	:	Plant secondary metabolites
ROS	:	Reactive oxygen species
TA	:	Titratable acidity
TAC	:	Trolox equivalence antioxidant capacity
TE	:	Trolox equivalents
TP	:	Total phenolics
TPTZ	:	2,4,6-Trispyridyl-s-triazine
TSS	:	Total soluble solids
TSS:TA	:	Total soluble solids to titratable acidity ratio
U of S	:	University of Saskatchewan
USDA	:	United States Department of Agriculture
UV	:	Ultraviolet

1. CHAPTER 1: INTRODUCTION

1.1 Background

Blue honeysuckle (*Lonicera caerulea* L. (Caprifoliaceae)) is a mesophytic shrub adapted to cold, northern climates (Plekhanova and Sokoleva 1992; Rudenberg and Green 1969a). Taxonomists have long recognized blue honeysuckle for its edible blue fruit that are harvested from the wild and in back-yard gardens as a traditional food source and medicine in Russia (Plekhanova 1998), Japan (Nakajima 1996), parts of China (Tang et al 2012) and eastern Europe (Juríková et al 2012a). Historically, blue honeysuckle was used to treat or prevent medical conditions in humans, ranging from arteriosclerosis, hypertension and liver disease to dropsy and indigestion (Kolasin and Pozdynakov 1991). In modern times, abundant flavonoid, especially anthocyanin, pigments as well as vitamin C and minerals have motivated its use as a fresh and processed food product (Sabitov 1986). For example, it is eaten fresh or frozen and used to make jam, juice, jelly, compote, syrup and natural dye by the residents of Siberia and the Russian Far East (Kolasin and Podzynakov 1991).

In the last two decades, arrival of genetic material from Eurasia and Japan to North America led to wide-spread interest in blue honeysuckle as a novel fruit crop for back-yard and commercial production (Thompson 2006a). Concurrently, blue honeysuckle gained recognition as a "superfruit" because of its high antioxidant content (reviewed by Celli et al 2014) and garnered attention in the scientific community despite the lack of epidemiological evidence connecting *in vitro* antioxidant potential to actual human health outcomes (Halliwell 2012). In addition to its presumed role in human health, blue honeysuckle has several outstanding features as a niche crop:

- Annual production of very early-season fruit, as much as two weeks earlier than even strawberries, depending on the region (Plekhanova 1994a);
- Extreme winter hardiness to -40 to -46°C while dormant (Imanishi et al 2000) and resistance to frosts of -8°C during bloom (Plekhanova 1989);
- Resistance to abiotic stresses, such as drought (Burmistrov 1994) and heat (Sabitov 1986), and to biotic threats from pests and diseases (Korobkova 2009);
- Unique flavor and aroma profiles (Thompson and Barney 2007) and a diversity of fruit shapes (Bors et al 2009);
- Adaptation to a range of cold northern climates and diversity of soil types (Plekhanova 2000);

- Low base requirements for horticultural management (Sabitov 1986; Kolasin and Podzynakov 1991);

- Abundant yellow flowers in the spring and green foliage that make it an attractive ornamental shrub (Thompson 2006b); and

- Synchrony of fruit ripening, permitting simultaneous harvest of all fruit (Thompson 2006b).

In regions where extreme winter cold, late spring frosts and a short growing season limit production of some commercial crops, blue honeysuckle stands out as an early source of spring nutrients (Plekhanova 1998). Despite its advantages in cold climates, blue honeysuckle production is limited in more temperate production regions where large-scale commercial fruit crop industries are well-established (Plekhanova 1994a; Zholobova and Khokhyrakova 2009). Specifically, as a recently domesticated novel crop, current cultivars have a combination of key genetic limitations:

- Modest peak yields (Plekhanova 1994a);

- Relatively small fruit size (Suzuki et al 2007);

- Low ratios of total soluble solids (TSS) to titratable acidity (TA) (Thompson 2006b);

- Unappealing or strange flavor profiles (Sarja 1998) or bitterness (Anikina et al 1988a);

- Thin skin and soft flesh resulting in delicate fruit quality (Sarja 1998), slow rate of manual harvest (Nakajima 1996), rapid loss of firmness after harvest (Ochmian et al 2008) and limited shelf life (Zholobova and Khokhyrakova 2009);

- Unsuitable growth habits for mechanized harvest (Kanarsky et al 2013), overly tight fruit attachment (Thompson and Barney 2007) or incomplete synchrony of ripening (Gudkovskiy et al 2009), hindering simultaneous harvest of fruit due to pre-harvest shattering (Sarja 1998);

- Self-incompatibility that necessitates inter-planting of three or more cross-compatible cultivars, reducing production efficiency (Khokhyrakova 2004);

- Tendency to sustain foliar damage and enter early dormancy in environments with long, hot summers (Bors et al 2012);

- Limited adaptation to temperate climates due to a low chilling requirement (Plekhanova 1994a), resulting in early bud break and death during the winter under fluctuating dormant-season temperatures (Sheyko 2009); and

- An early bloom period when low pollinator activity inhibits fruit set (Thompson 2006a).

With on-going improvements through breeding (Bors et al 2015), the crop has limitations in phenological adaptation to temperate climates, general agronomic performance compared to

large-scale commercial crops and biochemical aspects of fruit quality (e.g., low sugar to acid ratio) (Thompson 2006a). These factors restrict the potential for large-scale crop production. Compared to fruit crops with longer histories of breeding, research and market development, high cost of production perpetuates low market awareness for blue honeysuckle. With nascent industries in every Canadian province, growers face challenges to machine harvesting, packing, processing and marketing. As new cultivars enter the market, improvements in these traits are essential to long-term commercial success. Blue honeysuckle fruit characteristics limit future capacity for efficient production and wide-spread market availability, while public awareness depends primarily on genetic improvement through plant breeding. In turn, long-term success in breeding relies on thorough characterization of genetic resources to develop strategies to meet specific breeding objectives. Therefore, development of blue honeysuckle as a large-scale commercial crop for temperate climates relies upon determining variability and complexity of phenological adaptation, agronomic potential, fruit quality and nutritional content within and across foundation and improved germplasm groups.

1.2 Hypothesis

Across blue honeysuckle germplasm, there is variability and complexity of phenological adaptation, agronomic potential, fruit quality and nutritional content that can be used to develop a large-scale commercial horticultural crop for temperate climates.

1.3 Objectives

The long-term goal of this research is to expand the commercial potential of this cold climate crop for temperate climates using coastal British Columbia as an example of this target environment. There were three specific objectives for phenological traits associated with local adaptation, fruit morphological traits related to agronomic potential and fruit biochemical traits underlying fruit quality and nutritional content:

- Characterize genetic diversity in three distinct foundation germplasm groups;
- Assess potential for genetic progress in three improved germplasm groups; and
- Understand the physiological and genetic complexity of economically important phenotypic responses to a temperate coastal climate.

2. CHAPTER 2: LITERATURE REVIEW

2.1 Blue Honeysuckle as a Novel Fruit Crop

2.1.1 Introduction to the Crop

Blue honeysuckle is a novel fruit crop comprised of the polymorphic, tetraploid ssp. of *Lonicera caerulea* L. in the Caprifoliaceae family (Plekhanova and Rostova 1994). The Japanese common name, "haskap", is most pervasive in Canada, and "honeyberry" is used extensively in the US. However, "blue honeysuckle" is the most wide-spread name globally and the most inclusive of crop genetic resources. Three phenotypically distinct foundation germplasm groups are sourced from Japan (ssp. *emphyllocalyx*), Russia (primarily ssp. *edulis* and *kamtschatica*) and the Kuril Islands (an uncharacterized taxon) (Bors et al 2009). As for a more recent germplasm source from the boreal belt of North America (spp. *villosa*), the geographic ranges of these foundation groups are largely cold continental climates (Pojarkova 1958) (**Figure 2.1**).

Blue honeysuckle crop development began in Russia in the 1950's (Sabitov 1986) and in Japan in the 1960's (Nakajima 1996), but a rapid increase in global interest over the last two decades began with importation of germplasm to North America. This trend is attributed to the extremely early phenology and cold hardiness of the crop as well as the fruit's high antioxidant content, unique flavour profile, diversity of oblong shapes and utility as a fresh or processed product (Thompson and Barney 2007). In North America, university-sponsored breeding efforts are led by Dr. Maxine Thompson, professor emeritus at the Oregon State University, working out of Corvallis, Oregon, USA (Thompson 2006b) and Dr. Bob Bors at the University of Saskatchewan (U of S) in Saskatoon, Canada (Bors et al 2009).

Ongoing genetic improvements are increasing scientific and public awareness of blue honeysuckle, and the crop is poised on the edge of moving from the niche-market into the mainstream (Bors et al 2015). A major limitation to large-scale commercial production is lack of phenological adaptation to temperate climates for most blue honeysuckle germplasm (Thompson 2006a). For this reason, breeding in Oregon utilizes solely Japanese genetics, which are the most readily adaptable to the warm-summer Mediterranean climate (*Csb*) with dry summers and mild temperatures in Corvallis (Thompson 2006a). Characteristics of all three foundation germplasm groups are exploited in breeding efforts in a cold continental climate (*Dfb*) at the U of S (Bors et al 2012). In addition, this program is the first to systematically employ wide-cross hybridization between all three foundation groups to generate improved germplasm groups (Bors et al 2009).
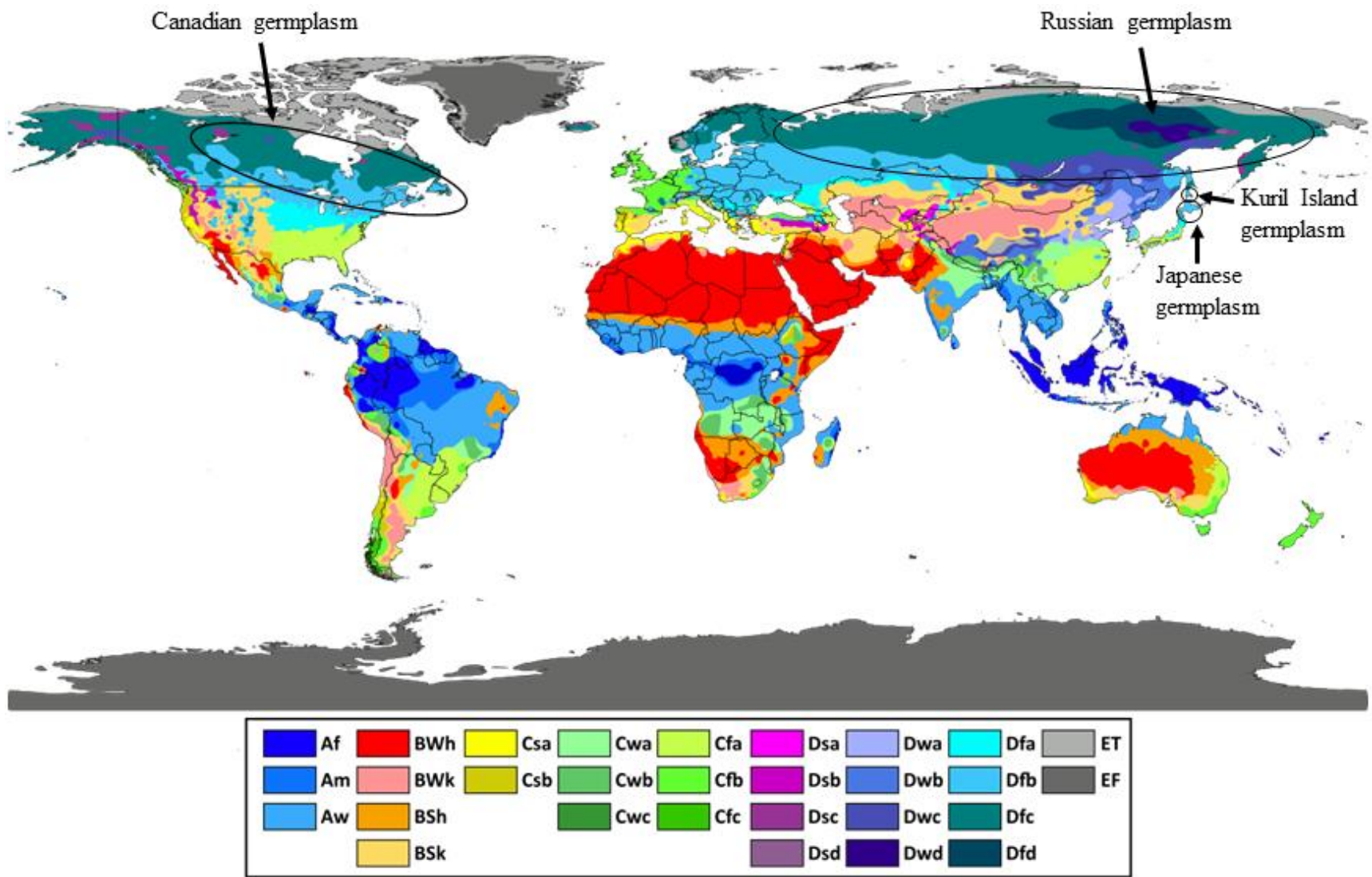
Figure 2.1. World map of the Köppen-Geiger climate classifications (Peel et al 2007) showing general provenances for major blue honeysuckle germplasm groups (adapted from Pojarkova 1958; Bors et al 2012).

2.1.2　Unique Fruit Ontology

As a woody perennial shrub (**Figure 2.2**), the central architecture of skeletal branches produces mixed buds on each season's new growth (Prischepina 2000). When these mixed buds break in the spring, the new shoots bear pairs of inflorescences at the base of one to three nodes (Kolasin and Pozdynakov 1991). Though the basic inflorescence for *Lonicera* is a simple three-flowered cyme, the central flower is usually suppressed in blue honeysuckle, resulting in a biflorate inflorescence (Rehder 1909). The corollas of these twin flowers are five-lobed, tube-shaped and pale yellow to cream in colour (Thompson 2006b). After bloom, the fruit resembles a simple berry at first glance, but it is comprised of two simple fruit enclosed in non-fruit tissue (Arber 1903), which fuses with the adjacent ovaries of these two flowers (Rehder 1909). *L. caerulea* is noted as unique in its genus for this surrounding bracteolar cupula that grows as the fruit matures, becoming pigmented and juicy at ripening (Rehder 1903). Therefore, blue honeysuckle is a compound accessory fruit resulting from synanthy of two flowers in an inflorescence (Pojarkova 1958).

Fruit colouring commences at the bottom of each branch where the earliest flowers bloom, proceeding rapidly to the next one or two fruit-bearing nodes (Nakajima 1996). There is a diversity of fruit shapes, including oblong, cylindrical, ovate, pear, bell, spindle, bottle and torpedo with individual fruit weights ranging from 0.4-1.5 g in Russian and 0.5-2.0 g in Japanese genotypes (Thompson 2006a) (**Figure 2.3**). The fruit possess an array of flavors described as sweet, sweet-sour, sour-sweet, sour or astringent with or without varying degrees of bitterness (Plekhanova 2000). Fruit colours range from deep purple to light blue depending on the degree of waxy cuticle (i.e., bloom), and ripeness follows full fruit colouring within three to five days (Thompson 2006a; Nakajima 1996). The anthocyanin pigments contained in the outer layers of the cupula would appear reddish-purple to black in color if not for this waxy cuticle (Skvortsov 1986). The compound, accessory nature of blue honeysuckle's unique fruit morphology (**Figure 2.4**) is the basis for both its diversity in fruit shapes and its high levels of antioxidant pigments found in multiple tissue layers. Combined with its dessert-quality flavor profiles, these features are central to amateur and scientific interest in blue honeysuckle around the world.

2.1.3　Basic Genetics and Taxonomy

Blue honeysuckle genetic resources include a collection of closely related taxa within subsection Caeruleae, but *L. caerulea* is typically given as the Latin name. With a basic
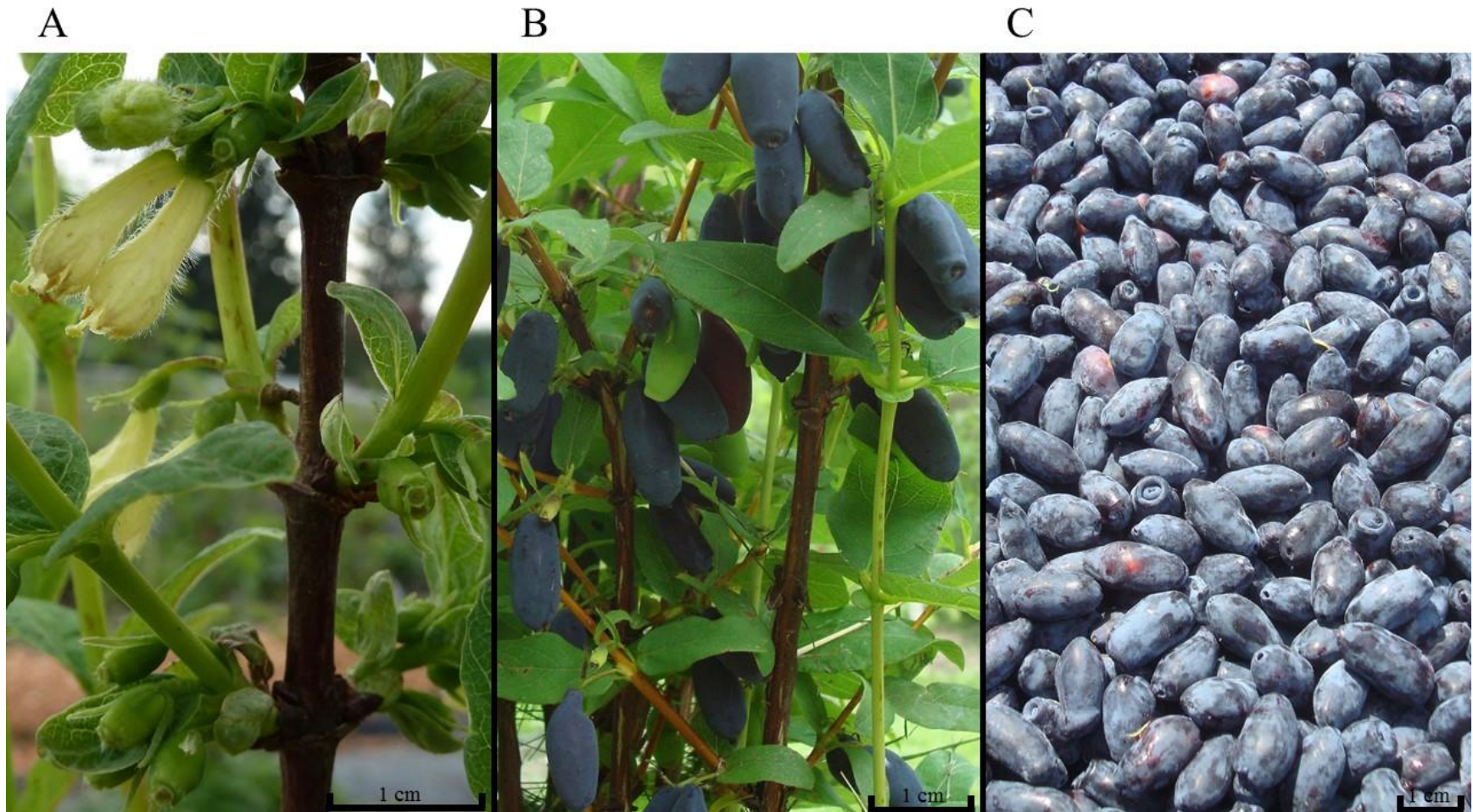
Figure 2.2. Blue honeysuckle, a novel blue fruit crop. (A) New spring growth with flowers and developing fruit (B) Ripe fruit on the bush (C) Harvested fruit.

Figure 2.3. Diversity in blue honeysuckle fruit shapes and sizes. (A) Oblong (B) Cylindrical (C) Ovate (D) Pear (E) Bell (F) Spindle (G) Bottle (H) Torpedo.

8

A

B

Fruit-pedicel
junction (bracts
included for
orientation)

Twin simple fruit

Location of false
fruit synanthy

Accessory layer of
bract tissue

Fruit calices

Termination of
accessory layer
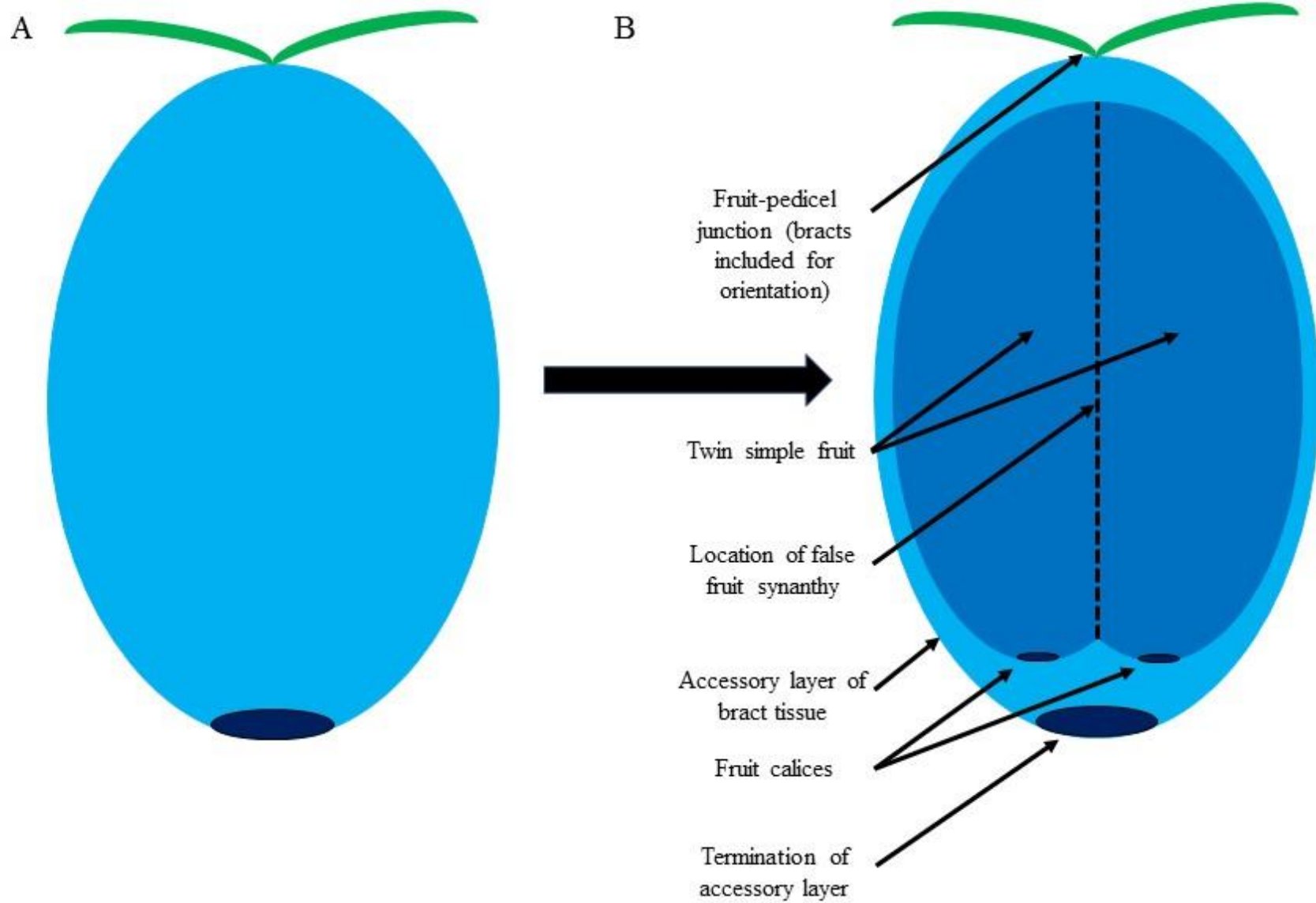
Figure 2.4. Idealized gross anatomy of blue honeysuckle fruit. (A) Exterior view (B) Cross-sectional view.

chromosome number of nine, most *Loniceran* species are diploid (2n = 2x = 18), but subsection Caeruleae is predominated by tetraploids (2n = 4x = 36) (Rudenberg and Green 1969a). The Eurasian representatives of the subsection include *altaica*, *baltica*, *buschiorum*, *caerulea*, *edulis*, *emphyllocalyx*, *iliensis*, *kamtschatica*, *pallasii*, *boczkarnikovae*, *stenantha*, *turczaninowii* and *venulosa*, while the North American taxa include *villosa* and *cauriana* (Plekhanova and Rostova 1994). There is taxonomic controversy as to whether the various tetraploid taxa ought to be considered species, subspecies or varieties, but the most consistent viewpoint is that these tetraploid taxa are all eco-geographic subspecies of *L. caerulea*. Further, though both diploid and tetraploid taxa are included in the germplasm collections of many breeding programs, neither diploid taxa nor tetraploid taxa outside the *L. caerulea* subspecies complex are recorded in cultivar pedigree records in the literature (M. Thompson, pers. comm. 2015-12-21).

The three diploid taxa of the subsection are likely the ancestral forms, which is supported by karyotypic similarities and their geographical distribution compared to the numerous, highly polymorphic tetraploid eco-geographic taxa (Plekhanova et al 1992). The center of diversity for subsection Caeruleae is Vavilov's East Asian center of plant origin, in the Russian Far East and central China (Sabitov et al 2007). High levels of fertility result from inter-hybridization between taxa of the same ploidy within the subsection in both the wild and the laboratory, while inter-ploid crosses result in low viability (Plekhanova 1994a). Even beyond subsection Caeruleae, crosses between species from distant reaches of *Lonicera* often result in viable hybrids (Plekhanova 2000). For example, crosses between *L. caerulea* ssp. *emphyllocalyx* and *L. gracilipes* can yield viable hybrids, though they may require the assistance of embryo rescue (Miyashita et al 2010). This suggests that genetic or cytological barriers were most likely not the cause of speciation during diversification (Rudenberg and Green 1969a). Therefore, polyploidization likely increased the ability of blue honeysuckle to adapt to a range of environments during adaptive radiation (Truta et al 2013).

2.1.4 Native Distribution

Blue honeysuckle has a circumpolar geographic distribution, being found mostly in the boreal and arctic forest belts of Eurasia where it grows as a woody perennial bush, 0.5 to 4.0 m in height (Rudenberg and Green 1969b). More specifically, the continental Eurasian wild forms range across Okhotiya and Yakutia; the Kamchatka and Kola peninsulas; the Sikhote-Alin,

Sayany, Altay, Ural and Amur mountains; the Ob, Pechora and Severnaya Dvina river valleys; and the Xeilongjiang and Xinjiang provinces of Northern China as well as Tajikistan, Kirghiziz and Kazakstan; and in Scandinavia and the Caucasus, Carpathian and the Alp mountain ranges of Europe (Plekhanova 2000; Sabitov 1986). In addition to the Kuril Islands in the north Pacific (Plekhanova 2000), wild relatives of cultivated Japanese forms are found in Hokkaido, Japan's northern island, as well as the Yamagata, Akita, Shizuoka, Nagano and Tochigi prefectures of Japan's main island, Honshu (Nakajima 1996). Though wild fruit is bitter throughout most of this native distribution, Kamchatka, the Okhotsk Sea coast, Sakhalin Island, Amur and the Transbaicalia region are sources of sweet, palatable fruit (Skvortsov 1986) as are the native ranges in Japan (Nakajima 1996). In North America, where one common name is "sweet-berry honeysuckle", blue honeysuckle grows in most Canadian provinces and northern parts of the United States (Fernald and Kinsey 1943).

The primary distribution of the blue honeysuckle is in boreal and temperate coniferous woodlands, scrub, fens and marshes as forest undergrowth (Mucina 1997). As is typical for northern circumpolar Lonicerans (Rudenberg and Green 1969b), it is restricted to river valleys, boreal groves and forest islets extending into the tundra at its northern limits and up to mountain timberlines at its altitudinal limits (Skvortsov 1986). Conversely, it is restricted to the upper half of the forest belt and, when protected, the lower parts of the subalpine and alpine belts at its southern extremes (Rudenberg and Green 1969b).

2.2 Phenological Adaptation to Temperate Climates

2.2.1 Climates of Native Range

Russian blue honeysuckle germplasm comes from a very broad geographic range across Eurasia, but the Kuril and Japanese germplasm have more restricted provenances. Based on the Köppen-Geiger climate classification (KGCC), ssp. *edulis* and *kamtschatica* provenances are characterized as continental climates with cold summers and either no dry season (subarctic climate – *Dfc), a* dry winter (monsoon-influenced subarctic climate – *Dwc*) or a dry summer (dry-summer subarctic climate – *Dsc*) (Peel et al 2007) (**Figure 2.1**).

As the primary source of blue honeysuckle germplasm from the Kuril Islands, Iterup (45° N 147° E) has a much milder (*Dfc*) climate than continental Russia with average minimum winter

temperatures of -8°C and high snow fall that protects plants from winter damage (Sabitov et al 2007; Peel et al 2007).

Wild germplasm was collected from throughout Hokkaido, but most Japanese germplasm used in North American breeding programs was obtained from the Bibai (43° N 141° E) and Chitose (42° N 141° E) regions, which are near Hokkaido's capital city, Sapporo (Nakajima 1996). Average high and low temperatures at Sapporo range from -0.6°C to -7°C (average 3.6°C) in January to 26.4°C and 19.1°C (average 22°C) in August, while precipitation ranges from 113 mm in January to 46.8 mm in June for an annual total of 1,107 mm (Climate Statistics 2012). Sapporo has a hot-summer humid continental climate (*Dfa*) with a wide range of temperatures, but the surrounding region has a warm-summer humid continental climate (*Dfb*) characterized by somewhat warmer summer temperatures (Peel et al 2007).

2.2.2 Basic Crop Requirements and Limitation on Temperate Climate Adaptation

Insufficient summer heat, strong frosts and poor soils determine the northern limits of blue honeysuckle distribution in the wild. However, excessive heat and drought limit its southern extremes (Sheyko 2009). Therefore, the fruit is recommended for cultivation as an early-season fruit in the colder regions of Russia specifically because of its northern adaptation and extreme winter hardiness (Sabitov 1986). In contrast, cultivation in temperate climates is generally limited by most cultivars' low chilling requirement that results in premature bud break during the winter and subsequent plant death or poor fruit set (Plekhanova 1986; Thompson 2006b).

In its northern native distribution, blue honeysuckle does not have strict requirements for specific soil conditions (Renata 2001) and needs neither a warm climate nor long growing season (Plekhanova 1994a). Fertile, medium textured soils with high organic matter and a pH slightly above 6.0 are preferable, but it can be cultivated on a wide range of soil types (e.g., well-drained sandy or loamy soils to heavy clay or peat soils) and pH's (4.5-7.5) (Plekhanova 1998). Similarly, it can tolerate wet soils but not prolonged flooding (Kolasin and Pozdynakov 1991).

Blue honeysuckle prefers full sun, for optimal fruit set during its early-season bloom period, but partial sun is also tolerated (Plekhanova 2000). When environmental conditions are conducive to insect activity, blue honeysuckle flowers have abundant nectar, which is an attractive food source for pollinators (Řezníček and Salaš 2004; Bozek and Wieniarska 2006). For this out-crossing, gametophytically self-incompatible crop to achieve adequate seed set to stimulate full

fruit development, at least two cross-compatible cultivars with overlapping bloom periods must be inter-planted (Plekhanova 1994a). Three to five cultivars are recommended to assure maximal fruit size and yield (Khokhryakova 2004). The sole cultivar from Japan, 'Yufutsu', has a high degree of self-fertility (Tanaka et al 1994), while a low degree of fruit set is observed in other blue honeysuckle representatives even when pollinators are scarce, which may be attributed to a low degree of parthenocarpy or incomplete self-incompatibility or both. Also, its low chilling requirement results in bud break and secondary flowering during the late fall and winter months when temperatures fluctuate above and below freezing, leading to yield reductions in the following year (Kolasin and Pozdynakov 1991). Therefore, with hundreds of blue honeysuckle cultivars now available globally, the crop's principal strength (i.e., its extreme cold hardiness) is also the most significant barrier to its development beyond the status of a niche crop to that of a large-scale commercial crop with adaptation to temperate climates (Plekhanova 1989). Consequently, to enhance the commercial potential of blue honeysuckle, cultivars with adaptation to temperate climates must be developed to increase the range of conditions under which the crop can be cultivated (Bors et al 2015).

Studies of blue honeysuckle germplasm adaptation are typically limited to evaluations of local adaptation in breeding populations that lack one or more important foundation germplasm group, making it difficult to investigate genetic variability within and between groups. Also, subjective evaluations almost universally lack biological replication or direct comparison to large-scale commercial crops or both. Evaluations in Corvallis, Oregon provide a preliminary analysis of blue honeysuckle germplasm adaptation to a temperate climate (Thompson and Barney 2007). However, no studies are available that objectively quantify genetic variability for phenological adaptation for a broad range of germplasm in a temperate climate with a well-established fruit production industry.

2.3 Morphological Traits Related to Agronomic Potential

2.3.1 Propagation, Productivity and Growth Habit

Propagation by seed is achieved simply without stratification or scarification (Sorokin 2002), but cultivation with true-to-type cultivars requires clonal propagation (Plekhanova 1998). Vegetative propagation is best conducted using spring soft-wood cuttings just before lignification begins, which is approximately the same time as the fruit begin to change color (Zholobova and

13

Khokhyrakova 2009). Hardwood cuttings (Tanaka et al 2009; Mezhenskiy 2009) and tissue culture (Sedlák and Paprštein 2007; Bryksin 2009a) are also viable means of propagation, the latter being the most efficient on a large-scale and requiring genotype-specific protocols (Bryksin 2009b).

For a woody perennial, blue honeysuckle's juvenility period can hardly be considered long as most cultivars bear fruit in the first year after planting (Plekhanova 1998). Final bush height varies from 0.8 to 3.0 m (Plekhanova 2000), and growth habits range from upright to spreading or mounding (Thompson 2006b). After spending the first few years establishing a central structure of skeletal branches, most genotypes will reach their peak yields as early as the fifth or sixth year, but the plant continues to develop to its mature size and shape for ten to twelve years (Kolasin and Pozdynakov 1991; Plekhanova 1998). As for many perennial shrub species, peak yields are maintained until the plant obtains this mature growth habit, which leads to a stage with reduced productivity and vegetative vigour (Belosohov 2010).

Germplasm evaluations from Russia report a wide range in peak yields from 2-6 kg that depends on the genotypes, climatic conditions and production system used for the study (Plekhanova 1998; Prischepina 2000). Given a typical plant spacing of 1 m within rows and 3 m between rows, this translates to between 8-24 t/ha. Breeder evaluations in the third/fourth year are typical (Grizodub 2009). This is because yield in the first few years is very closely related to mature yields, though fruit size can be smaller and shape more variable in the first two years (M. Thompson, pers. comm. 2010-06-15). Moreover, in Russia, evaluations of productivity, fruit size and biochemical features are conducted between the third and eighth year after planting (Plekhanova 1992).

Fruit develop from pairs of mixed vegetative/reproductive buds on the previous season's growth (Kolasin and Pozdynakov 1991). Lateral bud arrangement is opposite, and each axil has a vertical series of one to four buds, most often three (i.e., primary, secondary, tertiary), the number of buds depending on the location on the stem and plant overall (Thompson 2006a). Both primary and secondary lateral buds have the potential to develop reproductive structures as does the single apical bud at the end of each stem (Wu 1997). The shoot that emerges from a mixed bud bears two to four pairs of inflorescences at each of one to three successive nodes of new growth (Kolasin and Pozdynakov 1991). In total, each mixed bud can produce from two to ten inflorescences, each of which can become a single compound accessory fruit (Renata 2001). The number of flowers

14

available for pollination on any one branch depends on the number of mixed buds to break down its length in the spring, the number of nodes with flowers on each new shoot and the number of flower pairs per node (Plekhanova 1989).

Consequently, plant productivity is directly related to the amount of vigorous growth in the previous year, which sets mixed buds for the following season's crop (Prischepina 2000). The amount of vigorous new growth is related to the age of the skeletal branches, formed from vigorous shoots (i.e., whips) arising from dormant vegetative tertiary buds on older wood near the crown and growing 0.5 to 0.9 meters in a single season (Renata 2001). Alternatively, these vigorous shoots may arise from adventitious buds on the roots as suckers, though this is more commonly in taxa such as *L. caerulea* ssp. *altaica* and *pallasii* (Plekhanova 1989). These shoots are purely vegetative in the first year, but provide the new, productive wood that will develop mixed buds along their length for fruiting in the following years (Plekhanova 1989). Three- to five-year-old wood arising from these whips is the most productive, and, therefore, renewal pruning can maintain a state of productivity for 10 to 15 years (Kolasin and Pozdynakov 1991) by replacing older, unproductive skeletal branches with young whips and suckers from the base of the plant (Khokhryakova 2004).

2.3.2 Cultural Management Requirements

Most of the currently available production and management guidelines (Sabitov 1986; Plekhanova 1989; Kolasin and Pozdynakov 1991; Plekhanova 2000; Renata 2001) were developed in Russia for application to small-scale commercial operations or back-yard garden production. For this reason, blue honeysuckle has received much attention for its potential use in low-input or organic management systems (Bors 2009). The underlying assumption for these production systems is a relatively low intensity of management and flexible expectations for fruit yield and quality, which does not translate to large-scale production. Therefore, indications of blue honeysuckle's modest demands for irrigation, fertility and integrated pest and disease management should not be applied to the context of commercial horticulture (Renata 2001).

For example, basic plant growth is possible without supplemental fertilizer application (Plekhanova 1994b), but fertilization is required for commercially efficient levels of fruit yield and quality (Szot and Lipa 2012; Plekhanova 1998). Further, although application of organic manures or composts may provide plants with base nutrient requirements in high fertility soils,

heavier applications of synthetically-derived fertilizers are needed to obtain maximal plant growth and optimal fruit yield, size and quality (Plekhanova 1998).

Similarly, some soils and climates permit fruit development and plant survival without supplemental irrigation, but optimal production depends on a consistent water source, especially during bloom and fruit sizing (Matuškovič and Pokorná-Juríkova 2007). Blue honeysuckle is recommended for use in drought prone regions in Russia such as Altay, Siberia and the Urals because of its ability to ripen its early-season fruit before soils have completely dried out, reducing dependence on supplemental irrigation (Sabitov 1986). However, in most regions where water is available, application by drip or overhead sprinkler is recommended to maintain adequate plant water status and facilitate fruit development (Zhidyokhina 2009).

Moreover, though many sources indicate that blue honeysuckle is naturally resistant to pests and diseases (Korobkova 2009; Sabitov 1986; Thompson and Barney 2007), others emphasize the range of pests (e.g., aphids, moths, scale, chafers) and diseases (e.g., botrytis, powdery mildew) to which blue honeysuckle is susceptible (Plekhanova 1988; Naumova 2009). Birds are widely considered the most damaging pest, entire fields requiring netting in many cases (Bors et al 2009; Ryabinina 2009; Esichev 2009). Aside from the necessity of bird management, the potential to manage the crop using an organic, low-spray or no-spray program relates directly to the relative low intensity of back-yard garden and small-scale commercial production typical for this niche-market crop. In contrast, for large-scale production, it is necessary to employ an integrated pest and disease management plan using a range of horticultural tools (Tanaka et al 1994). This is especially true in regions with established fruit crop industries and the potential for cross-over of devastating pests such as the spotted wing drosophila, which was recently found in blue honeysuckle in Oregon (Lee et al 2015).

2.3.3   Evaluating Diversity in Fruit Morphology and Agronomic Potential

A diversity of fruit shapes (e.g., oblong, cylindrical, oval, ovate, pear, bell, jar, spindle, pod, bottle and torpedo) and sizes are reported, the latter ranging from 0.4-1.5 g to 0.5-2.0 g in Russian and Japanese germplasm, respectively (Thompson 2006a). Variability is reported for numerous fruit morphological features related to agronomic potential, including occurrence of incomplete synanthy that result in misshapen fruit (Ashimov et al 2009); degree of fruit surface smoothness (Plekhanova 1989); presence of pubescence on the fruit (Plekhanova 1989); heaviness

16

of the waxy cuticle (i.e., bloom) (Thompson 2006a); consistency of exterior colour (Ochmian et al 2012); fruit shape in cross-section as a ratio of the width parallel and perpendicular to the frontal plane (Plekhanova 1988); size and form of the accessory capsule as it terminates at the fruit's distal end (Plekhanova 1988); heterogeneity in fruit shape and size (Thompson and Barney 2007); firmness or consistency of the flesh (Ochmian et al 2012); strength of fruit attachment to the plant (i.e., ease of harvest) (Kanarsky et al 2013); tendency of the pedicels (i.e., stems) to detach with the fruit, contaminating the harvest (Rybnickova 2011); and size and quality of the picking scar (Gudkovskiy et al 2009).

Numerous cultivar descriptions are available to compare one or more of these agronomic traits across cultivars or selections (Plekhanova 1989; Tanaka et al 1994; Clark and Finn 2006; Kuminov 2009; Fefelov 2009; Il'in and Il'ina 2009; Zholobova and Khokhyrakova 2009). Germplasm evaluations for fruit morphology are reported from Russia (Plekhanova 1992; Hayrova 1996; Prischepina 2000; Teplyuk 2000; Khokhyrakova 2004; Savinkova and Gagarkin 2009; Savinich 2015), several Eastern European countries (Grizodub 2009; Matuškovič et al 2009a; Malodobry et al 2010; Ancu et al 2011; Ochmian et al 2013; Gawroński et al 2014) and Japan (Tanaka et al 1994; Takada et al 2003). A few of these studies include general indications of inheritance based on open-pollinated (OP) seedling populations, but none include analysis of all three important foundation germplasm groups or use methods such as mid-parent regression.

Of note, a preliminary observation of agronomic performance in a temperate climate in Corvallis, OR included all three foundation germplasm groups. Also, in a cold continental climate in Saskatchewan, the strengths and weaknesses of Japanese, Kuril, Canadian and Russian germplasm were evaluated with special focus on the latter (Bors et al 2012; 2015). These evaluations included categorical ratings for numerous fruit morphological features (e.g., fruit shape, ease of harvest, picking scar quality, productivity) in 17 Russian cultivars with calculation of selection indices for suitability to mechanical harvest, general appearance and taste. Generally, thorough characterization of genetic diversity for morphological traits is lacking in the literature.

2.4 Biochemistry of Fruit Quality and Potential Human Health Benefits

2.4.1 Key Contributors to Fruit Quality

Fruit quality (FQ) is influenced by a variety of biochemical attributes, but the relative importance of each depends on the end use of the product and the requirements of the consumer.

Total soluble solids (TSS) and titratable acidity (TA) are often central components of FQ, and their quantitative (by assay) or qualitative (by sensory panel) evaluation are essential to breeding programs (Diamanti et al 2011).

TSS is a major component of fruit dry matter (DM) and is measured in $^{\circ}$Brix or percent with a refractometer. TSS is highly correlated with sugar content, but other soluble compounds (e.g., organic acids and phenolics) also have influences (Cantwell 2014). For example, Cordenusi et al (2003) indicate sugar content from 5.4-9.4 corresponds with TSS of 6.9-10.3 in strawberry. Similarly, Ancos et al (1999) correlate sugar content from 9.26-10.54 with TSS from 14.59-17.98 in raspberry. The relation between TSS and perception of sweetness in the mouth is also influenced by the ratio of different types of sugars and their relative sweetness (Diamanti et al 2011). Relating to the perception of sourness, TA measures the total quantity of acids (organic and inorganic) available in a solution, whereas pH is the strength of the acidity of the solution. Combined, it is the balance between sweetness and sourness (i.e., TSS:TA), determined in the mouth, that facilitates the perception of aroma, by mouth and nose, and creates the over-arching sensation of flavour (Passam et al 2011). Specifically, high sugar/high acid yield high flavour; high sugar/low acid, sweetness; high acid/low sugar, tartness; and low sugar/low acid, blandness (Cantwell 2014). Accordingly, flavour is a complex trait, influenced by environmental factors, including climate and pre- and post-harvest management (Ulrich and Olbricht 2011).

2.4.2　Phenolics, Antioxidants and Human Health

Consumption of fruits and vegetables contributes to human health (Canada's Food Guide 2011). Specifically, fruit contain an abundance of vitamins, minerals, complex carbohydrates and plant secondary metabolite (PSM) compounds (Yahia 2010). Many small fruit crops are excellent sources of PSMs (e.g., anthocyanins and phenolic acids) that are recognized for their bioactivity as antioxidants (AOs) (Bakowska-Barczak et al 2007).

The role of AOs in the human diet relates to their functions in plants as scavengers of reactive oxygen species (ROS) – high energy molecules that act as second messengers but also cause cellular and genetic damage. The superoxide (SO) and hydroxyl radicals, hydrogen peroxide and singlet oxygen are major forms of ROS produced as regular by-products of cellular metabolism, through genetically programmed events in plant development (e.g., apoptosis) and in response to abiotic and biotic stresses (Foyer and Noctor 2005). To avoid stress triggers for ROS

production, plants have anatomical (e.g., leaf curling), physiological (e.g., C4 metabolism) and molecular (e.g., photosystem rearrangements) adaptations (Mittler 2002). Also, several mechanisms prevent accumulation of ROS-generating molecules, and scavenging of ROS is performed by enzymatic (e.g., SO dismutase) and non-enzymatic (e.g., ascorbic acid, polyphenols and carotenoids) means (Thomas 2000).

For the non-enzymatic means of ROS scavenging, anthocyanins are a non-enzyme class of polyphenol with a positively charged central ring that exist as water-soluble glycosidic compounds and impart a range of colours from red and blue to purple (Hou et al 2004). They are produced, transiently or permanently, in various plant tissues and in response to various developmental and environmental cues, abiotic stresses and changes in photoperiod and temperature (Chalker-Scott 1999). By filtering yellow-green and UV light, limiting ROS production, scavenging free radicals and facilitating osmoregulation, they act to kill microbes, repel herbivores and protect photo-labile defence compounds and the photosynthetic apparatus (Gould 2004; Stintzing and Carle 2004). Their AO activity (AOA) is due to the free radical-quenching hydroxyl groups on their aromatic rings that can produce resonance-stabilized phenoxyl radicals (Dudonné et al 2009). An anthocyanin's specific conformation affects its activity, and synergies between anthocyanins in heterogenous biological solutions make it difficult to evaluate their potency *in vivo* (Lila 2004)

In vitro animal cell studies provide a link between AO functions in plants and their potential human health benefits since AOs act as cellular protectants in both plants and animals (Lau et al 2006). This is important in humans because ROS production causes cleavage of DNA and cellular damage that lead to aging and cancer (Lau et al 2006). He and Giusti (2010) suggest that anthocyanins are: efficiently absorbed into the blood stream to be distributed to various tissues (Talavera et al 2003); decrease inflammation related to brain aging and neurodegenerative conditions (Shukitt-Hale et al 2008), risk of coronary heart disease (Renaud and de Lorgeril 1992) and severity of Type II diabetes (Ghosh and Konishi 2007); and increase night vision and contrast sensitivity (Muth et al 2000), inhibit cancer (Hou 2003) and help control obesity (Tsuda 2008). Therefore, demonstrating *in vivo* absorption, distribution and retention of anthocyanins, as well as associating their consumption with epidemiological outcomes, connects *in vitro* evidence with actual human health benefits.

2.4.3 Quantifying Phenolics and Antioxidant Activity

Characterizing foods with enhanced potential human health benefits requires elucidation of the specific quantities and conformations of the AO compounds they contain (e.g., Lee and Finn 2007; Wu et al 2004; Häkkinen et al 1999) and measurement of their AOA (e.g., Wong et al 2006; Velioglu et al 1998; Katalinic et al 2006). Several *in vitro* assays are available to compare relative AOA based on different chemical modes of action, but no one technique is universally applied because AOA depends upon experimental conditions and the combinations and quantities of AO compounds in solution (Zulueta et al 2009). Additionally, despite decades of study, there is conflicting evidence on the connection between *in vitro* and *in vivo* measurements of AOA and actual changes in the biomarkers of healthy human subjects, let alone reduced morbidity and delayed mortality on an epidemiological scale (Niki 2010). While there is some clear evidence of positive effects for subjects with compromised health or malnutrition (Halliwell 2012), the range of inference for studies of *in vitro* AOA remains limited to a potential, tentative connection with human health in otherwise healthy subjects.

Generally, AOA assays are either electron transfer (ET) assays, which measure the AOs' ability to reduce an oxidant, or hydrogen atom transfer (HAT) assays, which determine the AOs' ability to compete for a radical (Huang et al 2005). Simply, HAT assays are based on competition between the AOs and a substrate for a thermally generated radical, and ET assays are based on the AO's ability to reduce an oxidant, changing colour when reduced (Dudonné et al 2009). The ABTS (2,2'-asinobis diammonium salt) radical is the most widely used ET assay, whereas the oxygen radical antioxidant capacity (ORAC) assay, using peroxyl radicals produced by AAHP (2,2'azombis dihydrochloride), is the most prevalent HAT assay (Zulueta et al 2009). Other popular ET assays include the generic total phenolic (TP) assay, which uses the non-specific Folin-Ciocalteu (FC) reagent; AO scavenging of the DPPH (2,2-Diphenyl-1-picrylhydrazyl) radical; scavenging of the SO anion using the superoxide dismutase (SOD) assay; and the Ferric Reducing Antioxidant Potential (FRAP) assay, which uses ferric chloride (Fe^{3+}-tripyridyltriazine) (Huang et al 2005).

Each technique measures a different mode of AOA, and more than one assay is required to provide an accurate assessment of AO action. Correlation with other measures, high reproducibility and high throughput are important criteria for selecting methods for large numbers of samples (Huang et al 2005). The ORAC, FRAP, ABTS and DPPH assays were comparable for

guava germplasm (Thaipong et al 2006) and had good correlations across several other fruits and vegetables (Proteggente et al 2002). ORAC uses a more biologically relevant radical source, carries radical action to completion, quantifies activity with both percent and duration of inhibition, but the method is slow, reducing its utility for practical breeding applications (Prior and Cao 1999). In contrast, ABTS and FRAP are widely applied to plant extracts because they use simple equipment and are quick and reproducible with high correlations with TP (Thaipong et al 2006; Dudonné et al 2009). For example, ABTS and FRAP were highly correlated with each other and with total phenolics (TP) across numerous plant extracts (Dudonee et al 2009; Wong et al 2006), and ABTS was the most reproducible and easiest to implement in studies across laboratories using a variety of methods (Buenger et al 2006).

2.4.4   Potential Human Health Benefits of Blue Honeysuckle

Polyphenolics make up 0.4% of blue honeysuckle fresh weight, and four fifths or more of this polyphenolic fraction is comprised of anthocyanins (Palíková et al 2008). The fruit also contain high levels of hydroxycinnamic, chlorogenic and neochlorogenic acids as well as quercetin (Chaovanalikit et al 2004). Cyanidin-3-glucoside and cyanidin-3,5-diglucoside are the two major anthocyanins; however, cyanindin-3-rutinoside and cyanidin-3-gentiobioside present minor fractions (Terahera et al 1993), as do cyanidin-3-galactoside, peonidin-3-glucoside, cyanidin-3-xyloside and pelargonidin-3-glucoside (Bakowska-Barczak et al 2007; Oszmiański et al 1999). The proportion of cyanidin-3-glucoside is reported as high as 92.0% of total anthocyanins (Polina and Efremov 2015).

As reviewed by Juríková et al (2012b) and Celli et al (2014), blue honeysuckle's phenolic profile, AOA and potential human health benefits are reported based on *in vitro* and *in vivo* (animal) studies with comparisons to other crops (Rupasinghe et al 2012; Tomankova et al 2014). The significant human health benefits of blue honeysuckle include its antimicrobial (Raudsepp et al 2013), anti-inflammatory (Jin et al 2006), photo-protective (Svobodová et al 2008), anti-tumorigenic (Gruia et al 2008) and anti-arthritic (Wu et al 2015) properties as well as its potential to prevent cardiovascular disease (Jurgoński et al 2013), diabetes (Li et al 2009) and cellular oxidative damage (Bonarska-Kujawa et al 2014). The only human nutritional trial to date (Heinrich et al 2013) showed no clinical, biochemical or hematological effects on oxidative status in response to consumption of fresh blue honeysuckle. The only notable effect was an increase in

phenolic metabolites and AOA in the urine of the subjects. Therefore, further work is required to connect *in vitro* assays of blue honeysuckle AOA with actual human health outcomes.

Nonetheless, scientific interest in this niche crop's high vitamin C and polyphenol content have built on its reputation as a traditional therapeutic and prophylactic component of a healthy diet, leading to its recognition as a so-called "superfruit" (Makarov et al 2009). To date, there are few studies that use biological replication with direct field-based comparisons with large-scale commercial crops to understand the genetic variation in biochemical traits related to nutritional content. This information is required to validate wide-spread claims of the crop's potential to contribute to human health. Blue honeysuckle's plentiful phenolics and high AOA are central to the crop's growing popularity as a "superfruit", but relative comparisons to other fruits, vegetables and herbs vary dramatically across studies (Kusznierewicz et al 2012; Podędek et al 2014). Similarly, reports of vitamin C concentration range dramatically from 4.8-46.7 mg/100 g fresh weight (mg%) (Ershov 2009) to 9.71-92.29 mg% (Matuškovič et al 2009b) to 67.66-186.61 mg% (Juríková et al 2012b) though most studies rank blue honeysuckle highly compared to other crops (Plekhanova 1989). Also, mineral content varies considerably across reports (Tanaka and Tanaka 1998; Juríková et al 2012b; Rupasinghe et al 2012; Kusznierewicz et al 2012), but most indicate relatively high levels of potassium, calcium, phosphorus and magnesium (Shimoyama 2008; Palíková et al 2008).

2.5 Germplasm Evaluation and Blue Honeysuckle Crop Enhancement

2.5.1 Russia and Japan

Breeding began in Russia in the 1950's (Sabitov 1986), Japan in the 1960's (Nakajima 1996) and in the United States and Canada in the 1990's (Thompson 2006b; Bors 2009). Crop development in Japan was limited in scope, being restricted to the use of ssp. *emphyllocalyx* as foundation germplasm and ceasing entirely in the 1990's (Thompson 2006a). Extensive breeding efforts in Russia largely relied on selection of cultivars from OP seed collected from the wild and evaluated at research centers across Russia and several Eastern European countries (Kuklina 2009). The Eurasian ssp. *edulis* and *kamtschatica* were the primary foundation for these efforts. Subsequent generations of OP seedling evaluations, and more recent intentional hybridization of elite forms, have integrated other Eurasian subspecies to produce numerous cultivars (Hayrova 1996). Use of artificial hybridization between elite forms, rather than solely relying on OP seed,

is relatively recent for Russian breeding programs (Hayrova 1996), but wide crosses between Russian blue honeysuckle taxa (e.g., *kamtschatica* x *altaica* and *kamtschatica* x *edulis*) are also now employed in several regions (Zholobova and Khokhyrakova 2009). Finally, an uncharacterized taxon from the Kuril Islands is found in germplasm collections in Russia, Europe and North America (Plekhanova 1986). Its presence in the pedigree of several cultivars makes it an important third foundation germplasm group (Bors et al 2009).

As the basis for comparing blue honeysuckle cultivars in Russia and several Eastern European countries, the descriptor published by Plekhanova (1988b) is the earliest and most thorough reference for fruit evaluation of blue honeysuckle genetics. Based on this descriptor, germplasm evaluations are reported from numerous regions in Russia and several Eastern European countries. These evaluations generally focus on continental Eurasian subspecies, describing economically valuable phenological, morphological and biochemical traits in progeny lines without in-depth genetic analysis (Plekhanova 1992; Savinkova and Gagarkin 2009). Japanese and Kuril germplasm had superior adaptation compared to Russian germplasm when grown in a very wet (cold-moderate monsoon) climate outside the native range for blue honeysuckle (Sheyko 2009). Analysis of reciprocal crosses between Russian subspecies (*kamtschatica* and *altaica)* provides preliminary insight into combining ability in "dessert-quality" taste and yield (Il'in and Il'ina 2009). Several studies provide very basic information on the genetics of economically important traits in Russian germplasm from analysis of seedling populations (Hayrova 1996; Prischepina 2000; Khokhyrakova 2004; Suchkova and Senina 2009; Teplyuk 2000). This information is limited because most studies employ OP seedling populations to interpret general inheritance patterns, do not thoroughly quantify diversity between and within foundation groups and do not address improved germplasm groups at all.

General evaluation of adaptation and agronomic suitability is supplied from several regions across Russia (Ryabinina 2009; Esichev 2009; Razumnikov et al 2009; Golovunin 2009; Petrushua 2009; Murslimova 2013; Fefelov 2009; Stepanov 2009). In each of these studies from cold continental climates, location-specific information is not related back to the whole germplasm base, but is focussed on a narrow subset of germplasm and lacks any broad interpretation of the crop's genetic potential. Outside of Russia, studies with similar scope and inference are provided by researchers in Poland (Malodobry et al 2010; Ochmian et al 2013; Gawroński et al 2014),

Slovakia (Matuškovič et al 2009a), Romania (Ancu et al 2011) and Ukraine (Grizodub 2009; Mezhenskiy 2009).

In Japan, a range of phenological, morphological and biochemical traits were evaluated for the sole cultivar from Japan, 'Yufutsu', and several Japanese accessions (Tanaka et al 1994). In another study, intra-genotype correlations between morphological and biochemical traits showed a narrow genetic base for these traits (Takada et al 2003). Neither account provides relative comparisons to other foundation groups or analysis of the genetic control of these traits.

2.5.2   Oregon and Saskatchewan

The first thorough comparison of all three foundation germplasm groups was conducted in Corvallis, Oregon, with supporting data provided from the University of Idaho Research and Extension Center in Sandpoint, Idaho and the U of S in Saskatoon, Canada (Thompson and Barney 2007). This provides general inferences for the utility of foundation germplasm groups for developing cultivars that are well-adapted to temperate climates and possess early-ripening phenology, good FQ and high nutritional content. Poor temperate climate adaptation was noted for most Russian taxa and poor FQ for Kuril material, but the Japanese germplasm was discovered as a source of superior FQ and temperate climate adaptation. Wide genetic variability was observed for traits such as productivity, plant vigor, growth habit, phenological response to climatic conditions, harvestability and basic FQ. The authors suggest that all the ingredients for suitable cultivars were observed in one accession or another and that breeding was required to incorporate them into future cultivars. Consequently, breeding in Oregon relies entirely on ssp. *emphyllocalyx*, as in Japan (Thompson and Barney 2007). Using intentional crossing to make genetic improvements in traits such as total soluble solids and fruit size, rapid genetic gains over nearly two decades resulted in release of a first generation of cultivars with exclusively Japanese genetics (Thompson 2016).

In Canada, initial evaluations at the U of S provide basic comparisons of a broad range of blue honeysuckle germplasm, describing general variability within foundation groups and inferring their use in strategic breeding for a range of production regions (Bors et al 2009; 2012). These evaluations facilitated identification of key strengths and weakness in each germplasm group and development of strategies for crop enhancement by hybridization of complementary germplasm sources. Based on these evaluations, breeding at the University of Saskatchewan (U

24

of S) employs the broadest range of phenotypically distinct taxa from Russia (primarily ssp. *kamtschatica* and *edulis*), Japan (ssp. *emphyllocalyx*), the Kuril Islands (an uncharacterized taxon) and Canada (ssp. *villosa*) (Bors et al 2012). The Russian forms are adapted to the coldest climates and have the earliest phenology, presumably due to low chilling requirement (Plekhanova 1994a). The Kuril forms are low-growing with thick pubescence covering most plant structures and have much later phenology (Plekhanova 1986). The Japanese forms have intermediate phenology but greater adaptation to temperate climates (Thompson 2006a). The wild Canadian germplasm is low in stature and productivity with generally round-oval fruit (Bors et al 2012).

With the broadest set of germplasm resources available globally, the aim of the U of S program is to develop blue honeysuckle as a large-scale commercial crop with fresh and processed market potential. To achieve this objective, this broad range of phenotypically distinct taxa was used in controlled crosses to elucidate the genetic control of economically important traits in a temperate climate. Moreover, the U of S program is the first to extensively use wide crosses between all three of the crop's important foundation germplasm groups to generate improved germplasm groups with novel phenotypes (Bors et al 2012). This breeding strategy is intended for development of cultivars with hybrid vigour (i.e., heterosis) for traits that contribute superior agronomic performance (Bors et al 2015).

Heterosis is observed as a more extreme phenotype that transgresses beyond that of either parent (i.e., transgressive segregation), which is explained by theories of dominance, overdominance and epistasis (Acquaah 2007; Rieseberg et al 1999). Therefore, the U of S uses these wide crosses to bring together traits from different germplasm sources and produce transgressive segregants for important morphological, biochemical and phenological traits (Bors et al 2012). Key objectives are to develop machine-harvestable cultivars with superior flavour, utility for processing applications and a range of ripening periods (Bors et al 2012). Several hybrid cultivars were released from this program, including 'Borealis', 'Tundra', 'Indigo Gem', 'Indigo Yum' and, more recently, 'Aurora', 'Boreal Blizzard' and 'Boreal Beauty' (Bors et al 2015).

Motivation for the use of wide crosses is based on the genetic features of out-crossing crops. Specifically, blue honeysuckle has gametophytic self-incompatibility and requires cross-pollination for optimal fruit set (Plekhanova 1994a). Compounded by the crop's tetraploid genome, cross-pollination results in a high degree of heterozygosity and production of wide variation in allelic combinations in each generation (Acquaah 2007). Crosses between close

relatives results in inbreeding depression (i.e., exposure of deleterious alleles normally masked by heterozygosity), therefore, wide crosses are used to generate superior phenotypes with hybrid vigour that can be locked into perpetuity through clonal propagation (McKey et al 2010).

While superior cultivars with heterosis for desired traits can be produced in a single generation, long-term population improvement can only be realized through additive gene action, which permits accumulation of desirable alleles between and within loci (Acquaah 2007). This can be effected through recurrent mass selection to increase the concentration of desired alleles that can then be recombined through wide crosses between heterotic groups (i.e., germplasm groups that combine to generate phenotypes displaying heterosis) (Acquaah 2007). Consequently, for blue honeysuckle, there is a need to understand genetic variance as a proportion of total variance (i.e., broad-sense heritability), the proportion of variance due to additive gene action (i.e., narrow-sense heritability), the predominant modes of gene action controlling traits and the ways in which heterotic foundation groups combine to produce novel improved phenotypes. Evaluation of these genetic traits in a temperate climate is key to crop enhancement.

2.5.3 The Fraser Valley - A Temperate Climate Target Environment

The Fraser Valley is the 150-km long basin of the Fraser River as it flows into the Pacific Ocean in southwestern British Columbia (BC), Canada. It is the primary geographic feature of the Lower Mainland, which contains the city of Vancouver and its suburbs to the south and east. It reaches from Whatcom County, Washington in the south to the Coast Mountains in the north and is bounded to the east by the Cascade Mountains and to the west by the Georgia Straight. The Fraser Valley has a temperate oceanic climate (*Cfb*) that is characterized by a warm summer and no dry season (Peel et al 2007). Upper air westerlies exert strong control over weather patterns by bringing systems in from the Pacific Ocean: high pressure systems of hot, dry weather are punctuated by subtropical storms in the summer; and low pressure systems carry cold air and heavy precipitation, primarily as rain and occasionally as snow, in the winter (Maunders 1968; Bertrand 1991; Demarchi 2011). As one of the highest chilling regions in North America, microclimatic variation is influenced by distance from the Georgia Strait, altitude, slope and aspect, and plant hardiness zones are very mild (7a to 8a) (Bertrand 1991; McKenney et al 2001).

The Fraser Valley has a well-established horticulture industry and is a major production region for highbush blueberry and red raspberry with a long-standing, though now small,

strawberry industry. The province leads Canada in fruit production with more than 24,000 hectares producing 273,000 tonnes of fruit in 2015, generating more than $372 million in farm cash receipts and $508 million in exports (British Columbia Agri-Food Industry: Year in Review 2015). Therefore, this region is an appropriate target environment for evaluation of commercial potential for the blue honeysuckle under temperate climatic conditions, which will facilitate crop enhancement.

Understanding the underlying genetics of foundation and improved germplasm is an important objective because it is necessary for directing breeding efforts that overcome blue honeysuckle's current limitations as a niche crop and launching the next step in its development as a commercial fruit crop. These barriers are attributed to limited phenological adaption to temperate climates because of a low chilling requirement and tendency to break bud and bloom under very cold conditions when pollinators are relatively inactive (Plekhanova 1994a; Sheyko 2009); morphological traits associated with restricted agronomic potential such as low productivity and small fruit size (Plekhanova 1994a; Suzuki et al 2007); and fruit biochemical traits, such as unappealing flavour or sugar/acid ratio and limited shelf life and harvestability, that negatively impact FQ, and restrict marketability despite high nutritional content that contributes potential human health benefits (Sarja 1998; Thompson 2006a; Nakajima 1996; Zholobova and Khokhyrakova 2009).

3. CHAPTER 3: GENERAL MATERIALS AND METHODS

3.1 Germplasm Description

3.1.1   Foundation Germplasm

Initial evaluation of genetic variability in the University of Saskatchewan (U of S) germplasm collection led to selection of 24 accessions from three foundation germplasm groups (Russian, Japanese and Kuril) that were recently use in a wide-cross breeding strategy (**Table 3.1**). Seven Russian cultivars are primarily ssp. *kamtschatica*, but use of open-pollinated (OP) seed in Russian breeding programs makes it impossible to exclude ssp. *edulis* or other continental Eurasian subspecies from their background. R-27-35 is an OP *kamtschatica* seedling from Balsgaard, Sweden, likely with a minority of Kuril genetics in its lineage. Four of the five Kuril genotypes (K-3-03, K-3-05, K-3-06 and K-3-07) are closely related descendants of a single clone taken from Iterup Island for use in Russian breeding programs. The fifth Kuril type, K-97-12, likely has a minority of ssp. *kamtschatica* in its lineage, but it bears very strong resemblance to the other Kuril forms. The Japanese accessions were selected from seed lots imported to North America from several locations in Hokkaido. Out-group comparisons included three U of S hybrid cultivars ('Borealis', 'Tundra' and 'Indigo Gem'), offspring of K-97-12 and a *kamtschatica* cultivar ('Czech No. 17'), as well as an unnamed Japanese genotype, J-PP, imported by a Canadian nursery (Piroche Plants Inc., Pitt Meadows, BC).

3.1.2   Improved Germplasm

To compare with the 24 foundation genotypes, groups of four full-siblings (i.e., families) were selected from each of 40 seedling populations for a total of 160 improved hybrid genotypes. Three unique combinations of foundation groups were each represented by both directions of cross and treated as combined improved groups (i.e., Japanese x Kuril + Kuril x Japanese – Japanese/Kuril, Japanese x Russian + Russian x Japanese – Japanese/Russian, Kuril x Russian + Russian x Kuril – Kuril/Russian). Phenological differences between foundation groups affected the frequency of crosses in the program, resulting in half the number of improved families for the Japanese/Kuril group compared to the Japanese/Russian and Kuril/Russian groups (**Table 3.2**). The sampling procedure did not reflect a formal mating design but rather a representative sampling of the improved germplasm found in the active breeding program. Diversity was maximized within the constraints of the existing breeding populations, necessitating uneven representation of

Table 3.1. Genetic background and source for foundation blue honeysuckle genotypes and out-group comparison cultivars.

Background	Source	U of S Code	Thesis Code	Cultivar Name
Japanese[1]	USDA NCGR[5]	MT-21-78	J-21-78	n/a
Japanese[1]	USDA NCGR	MT-22-14	J-22-14	n/a
Japanese[1]	USDA NCGR	MT-41-83	J-41-83	n/a
Japanese[1]	USDA NCGR	MT-42-45	J-42-45	n/a
Japanese[1]	USDA NCGR	MT-43-87	J-43-87	n/a
Japanese[2]	USDA NCGR	MT-45-14	J-45-14	n/a
Japanese[2]	USDA NCGR	MT-46-55	J-46-55	n/a
Japanese[2]	USDA NCGR	MT-56-18	J-56-18	n/a
Japanese[2]	USDA NCGR	MT-66-53	J-66-53	n/a
Japanese[3]	USDA NCGR	MT-73-39	J-73-39	n/a
Japanese[4]	USDA NCGR	MT-444-39	J-444-39	n/a

Total Japanese Genotypes: 11

Background	Source	U of S Code	Thesis Code	Cultivar Name
Kuril	One Green World[6]	SX-3-03	K-3-03	Blue Pacific™ ('F-1-9-58')
Kuril	One Green World	SX-3-05	K-3-05	Blue Nova™ ('Novinka')[7]
Kuril	One Green World	SX-3-06	K-3-06	Blue Sky ('Valery No. 2')
Kuril	One Green World	SX-3-07	K-3-07	Blue Lightning™ ('Zarnitsa')[7]
Kuril	One Green World	SX-97-12	K-97-12	Blue Velvet™ ('Kiev #17')

Total Kuril Genotypes: 5

[1]OP seed from Bibai and Chitose regions of Japan.

[2]OP seed from Japanese selections grown in Corvallis, OR, USA.

[3]Japanese selection from controlled cross (Bibai x Chitose) in Corvallis, OR, USA.

[4]Japanese selection from Corvallis, OR, USA but of unknown origin in Japan.

[5]United States Department of Agriculture National Clonal Germplasm Repository, Corvallis, OR, USA

[6]Mail order nursery, Portland, OR, USA

[7]Mis-identified cultivar names based on pedigree records.

Table 3.1. Continued. Genetic background and source for foundation blue honeysuckle genotypes and out-group comparison cultivars.

Background	Source	U of S Code	Thesis Code	Cultivar Name
Russian	Vavilov Institute[8]	SX-2-06	R-2-06	'Morena'
Russian	Vavilov Institute	SX-2-07	R-2-07	'Nimfa'
Russian	Vavilov Institute	SX-2-10	R-2-10	'Lebedushka'
Russian	Vavilov Institute	SX-2-11	R-2-11	'Omega'
Russian	Vavilov Institute	SX-2-13	R-2-13	'Suvenir'
Russian	Vavilov Institute	SX-2-14	R-2-14	'Solovey'
Russian	Vavilov Institute	SX-2-16	R-2-16	'Slavyanka'
Russian	Vavilov Institute	MT-27-35[10]	R-27-35	n/a
Total Russian Genotypes:		8		
Japanese	Piroche Plants[9]	n/a	J-PP	n/a
Kuril/Russian	U of S	SX-9-94	KR-9-94	'Borealis'
Kuril/Russian	U of S	SX-9-84	KR-9-84	'Tundra'
Kuril/Russian	U of S	SX-9-15	KR-9-15	'Indigo Gem'

[8]St. Petersburg, Russia

[9]Wholesale nursery, Pitt Meadows, BC, Canada

[10]OP seed obtained from Balsgaard Botanical Gardens in Sweden.

Table 3.2. Blue honeysuckle improved germplasm and comparison crop cultivars compared in the Fraser Valley, BC, Canada. (A) Parental combinations, number of seedling families, siblings per family and total number of improved hybrid blue honeysuckle genotypes selected from the University of Saskatchewan germplasm collection (B) Cultivars of northern highbush blueberry, floricane-fruiting red raspberry and June-bearing strawberry with harvest period and typical market use.

A

Parental Cross Combination	Seedling Families	Siblings/ Family	Total
Japanese x Kuril	5	4	20
Kuril x Japanese	3	4	12
Total Japanese/Kuril	8		32
Russian x Japanese	8	4	32
Japanese x Russian	8	4	32
Total Japanese/Russian	16		64
Kuril x Russian	8	4	32
Russian x Kuril	8	4	32
Total Kuril/Russian	16		64
Grand Total	40		160

B

	Cultivar	Harvest Period	Fresh Market	Process Market
Blueberry	'Bluecrop'	Mid	✓	✓
	'Duke'	Early	✓	✓
	'Elliott'	Late	✓	
	'Reka'	Early		✓
Raspberry	'Cascade Bounty'	Late		✓
	'Chemainus'	Mid	✓	✓
	'Meeker'	Mid		✓
	'Saanich'	Mid	✓	✓
Strawberry	'Rainier'	Late	✓	✓
	'Puget Reliance'	Early	✓	✓
	'Stolo'	Mid	✓	
	'Totem'	Mid	✓	✓

foundation genotypes as parents of improved genotypes (**Appendix A.1**).

3.2 Field Trial Establishment and Management:

3.2.1 Plant Propagation and Comparison Crops

Softwood cuttings were taken during active growth from the blue honeysuckle germplasm collection and seedling populations at the horticulture field facility at the U of S in Saskatoon, SK on May 20, 2010. Clones of each genotype were rooted in a mist-bed then potted in Sunshine Mix #4 (Sun Gro Horticulture, Agawam, MA, USA). The first set of cuttings to root were grown in 11.4 cm deep (142 mL) plug trays (T.O. Plastics, Clearwater, MN, USA) to 25 cm of top growth then transported to the Fraser Valley for an initial planting on August 28, 2010. Subsequent clones were grown-on in 2.6 L #1 round pots (ITML Horticultural Products, Branford, ON, Canada) from September 1, 2010, to January 21, 2011. When plants had 45 cm of top growth, they were artificially induced to enter dormancy using short-day (8 h) photoperiod and $0\text{-}2^{\circ}C$ temperature until being transported to the Fraser Valley for planting April 16-18, 2011.

For comparison with blue honeysuckle, standard cultivars of northern highbush blueberry (*Vaccinium corymbosum* L.), floricane-fruiting red raspberry (*Rubus idaeus* L.) and June-bearing strawberry (*Fragaria* *x*ananassa* Duch.) were included to represent a range in phenology and market uses for each crop (**Table 3.2**). Dormant bare-root raspberry and strawberry plants were procured from Norcal Nursery Inc. (Burlington, WA, USA) and two-year-old blueberry plants in 2.6 L #1 round pots were obtained from JRT Nurseries Inc. (Aldergrove, BC, Canada). These crops were chosen for comparison based on their global economic importance as large-scale commercial crops as well as their prevalence in the Fraser Valley (British Columbia Agri-Food Industry: Year in Review 2015).

3.2.2 Field Trial Sites and Establishment

Three Fraser Valley farm locations were selected in the cities of Langley, Pitt Meadows and Chilliwack (**Figure 3.1**; **Table 3.3**). The soil at the Langley site is an Everett sandy loam characterized by a 20-cm reddish-brown layer of coarse, rocky soil over 25 cm of even lighter textured material above course grey sand that drains very quickly, limiting non-irrigated agricultural activity during summer months (Kelley and Spilsbury 1939). The soil at the Pitt Meadows site is a Ladner clay made from recent alluvial deposits with profile development

Figure 3.1. Map of foundation blue honeysuckle germplasm trials in the Fraser Valley (Google Maps, 2016). (A) Fraser Valley within British Columbia, Canada (B) Trial sites within the Fraser Valley.

Table 3.3. Description of three trial sites in the Fraser Valley used to compare blue honeysuckle foundation germplasm.

		Langley (49°07'N 122°33'W)	Pitt Meadows (49°14'N 122°42'W)	Chilliwack (49°08'N 121°56'W)
Precipitation (mm)[1]	Highest month	198	334	257
	Lowest month	37	72	54
	Yearly total	1,306	2,200	1,679
Average temperature in coldest month (^{o}C)	Maximum	6	54	5.2
	Minimum	-0.9	-0.7	-0.5
	Average	3.4	2.2	2.3
Average temperature in hottest month (^{o}C)	Maximum	24.1	23.5	24.5
	Minimum	13	11.9	12.2
	Average	18.5	17.6	18.4
Physical description[2]	Elevation (m)	62	3	15
	pH	6.5	5.4	5.6
	OM (%)	3.6	7.4	3.6
	Fertility	Low fertility; high in P and K	High fertility; high in P and K	High fertility; low in P and K

[1]Long-term precipitation and temperature averages from the previous ten-year period (The Weather Network 2012).

[2]Based on soil testing conducted March 15, 2012.

restricted to a 15-cm high organic matter layer over 1.1 m of grey clay that drains to sand underneath, resulting in high agricultural productivity (Kelley and Spilsbury 1939). The soil at the Chilliwack site is a Monroe clay loam with more than 30 cm of brownish-grey clay loam over silty loam and stratified layers of medium-textured sand beneath, making it highly fertile when properly drained (Kelley and Spilsbury 1939).

Contrasting with the range in cold continental climates (Köppen-Geiger climate classification (KGCC) – *Dfa*, *Dfb*, *Dfc*, *Dsc*, *Dwc*) of the foundation germplasm's native provenance (**Figure 2.1**), the Fraser Valley has a temperate oceanic climate (KGCC – *Cfb*) with abundant rainfall, mild winter temperatures and long growing season (Peel et al 2007). The plant hardiness zone is 8b for the Chilliwack and Langley sites and 8a for the Pitt Meadows site (Kramers et al 2014), but the Fraser Valley has important microclimatic variation. Temperature and relative humidity were recorded at half hour intervals using data loggers (Onset, Cape Cod, MA, USA) at each location in 2012 (**Figure 3.2**; **Appendix A.2**) and 2013 (**Figure 3.3**; **Appendix A.3**).

With individual plants as experimental units, randomized complete block designs with three replicates were established at all three sites to compare the 24 foundation genotypes with the comparison crops. Three blue honeysuckle guard plants were used at the start and end of each row. All plants used in these trials were transported from the U of S in April 2011. To compare improved germplasm with parental foundation groups, the Chilliwack site was used to establish a single-location trial. Three randomized blocks each contained 49 nested sub-plots with three randomized technical replicate clones of each of the four genotypes. There were 40 sub-plots for full-sibling improved genotypes, six for parental foundation genotypes and three for the comparison crops. There was a single guard plant at the start and end of each row and a full row of guard plants on either side of the trial. Plants transported in August 2010 were used to establish the first sub-replicate clone of each genotype per replication. Subsequently, plants transported in April 2011 were used to complete each sub-plot.

For all trials, spacing was 0.6 m within-rows. Between-row spacing was 3.0 m at the Langley site without hilled beds, and it was 1.8 m at the Pitt Meadows and Chilliwack sites with 0.5 m hilled beds. Row orientation was north/south in Langley and Pitt Meadows and east/west in Chilliwack. Inter-row spaces were managed by rototilling in Langley, Sunbelt woven ground cover (DeWitt Company Inc., Sikeston, MO, USA) in Pitt Meadows and mowed perennial
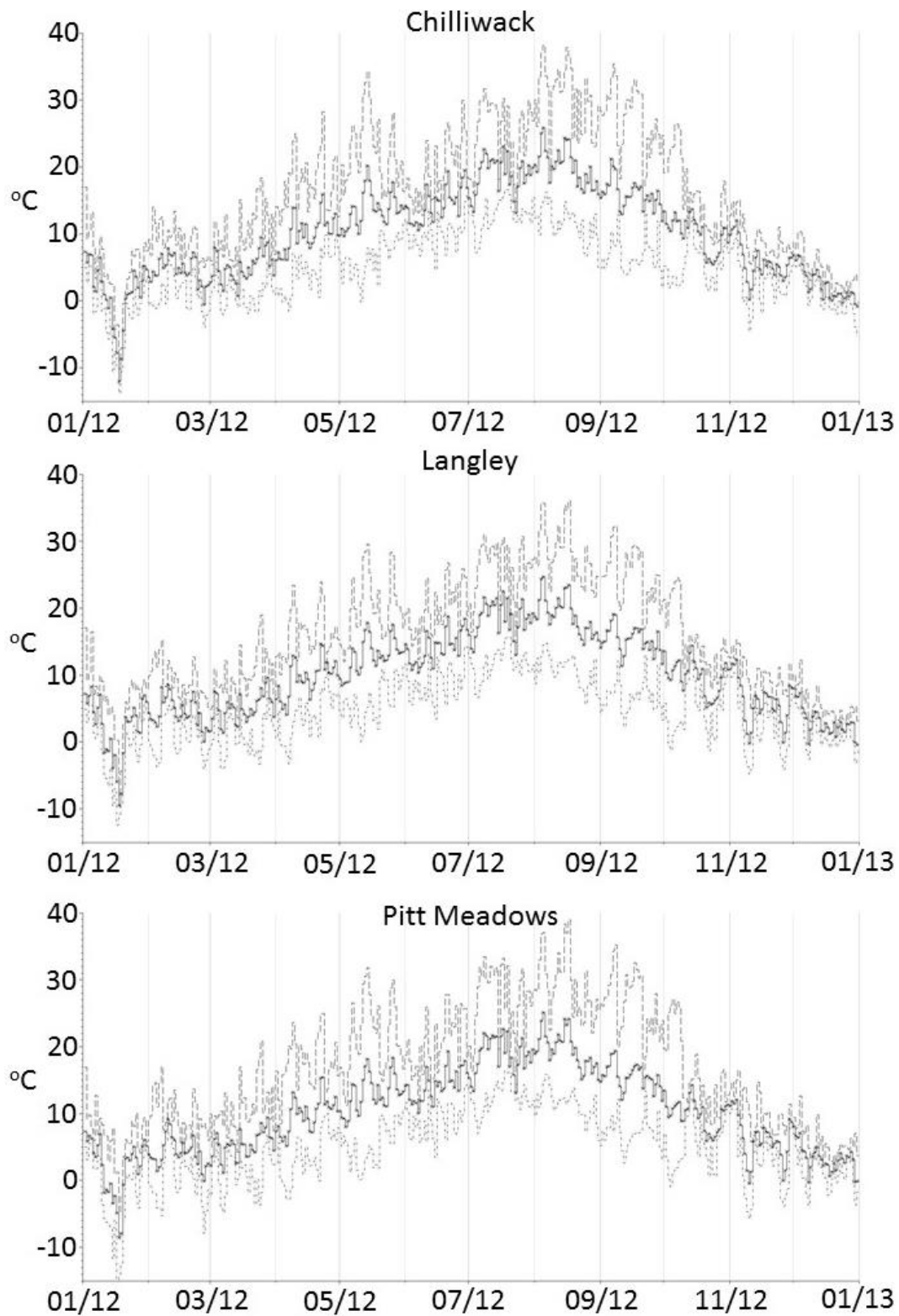
Figure 3.2. Temperature data for three trial sites in the Fraser Valley, BC, Canada in 2012 (Top line – daily maximum, Centre line – daily average, Bottom line – daily minimum).
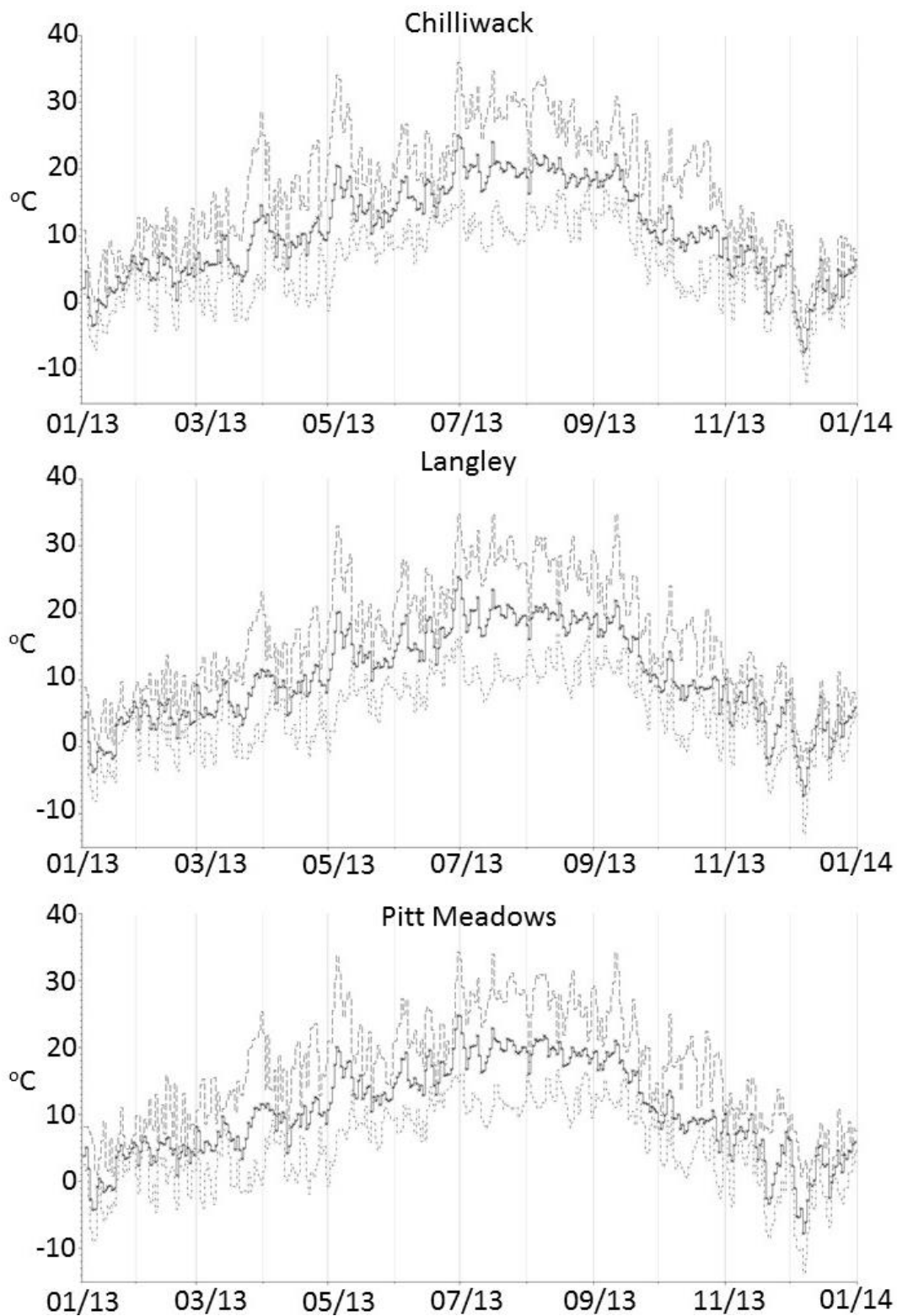
Figure 3.3. Temperature data for three trial sites in the Fraser Valley, BC, Canada in 2013 (Top line – daily maximum, Centre line – daily average, Bottom line – daily minimum).

grass in Chilliwack. All three sites were protected with bird netting during fruit development and harvest. An application of 200 g/L paraquat at a rate of 4.8 L/Ha (Syngenta Canada, Guelph, ON, Canada) was made on April 15, 2012, at the Chilliwack site. All other within-row weed management was performed manually. Suppression of weed seed germination was facilitated by an 8-cm layer of wood-chip mulch applied to all sites on April 25, 2012 (Ground Cover Services, Abbotsford, BC, Canada). No pesticides or fungicides were applied through the course of the experiment and irrigation was supplied through a single (Chilliwack and Pitt Meadows) or double (Langley) drip line per row. Based on the BC Ministry of Agriculture (2010) recommendation for highbush blueberry plants of equivalent size, split applications of fertilizer (18-12-12 + 1Ca 0.5Mg 5S and micronutrients [BioFert Manufacturing Inc., Abbotsford, BC, Canada]) were made at 47 g/plant on April 1 and May 1, 2012, and at 78 g/plant on March 28 and April 28, 2013. While the Langley and Pitt Meadows sites were surrounded with a diversity of berry crops and numerous commercial honeybee hives, pollination at the Chilliwack site was supplemented with four honeybee hives during bloom.

3.3 Phenological Observations

From January 2012 to December 2013, phenological development was observed every two to four days for individual plants in both the multi-site foundation and single-site improved germplasm trials. Julian dates were recorded for all determinations of phenophases from dormancy to fruit set (**Figure 3.4**) and fruit ripening to dormancy (**Figure 3.5**):

- Bud break, defined as the peeling back of bud scales and release of green tissues, was recorded upon opening of 10, 50 and 90% of buds (bud break phenology not collected for strawberry due to non-woody growth habit);
- Flowering onset, defined as the opening of the corolla for the first pairs of flowers on each new shoot, was recorded at first open flower and at 30 and 90% of new shoots with open flowers (also recorded for blueberry cluster, raspberry lateral and strawberry truss);
- Fruit colouring, defined as the fully blue coloration of fruit, was recorded at 50, 75 and 100%;
- Fruit harvest was based on a single, simultaneous harvest from each plant, three to five days after the 100% blue stage (multiple harvests are required for blueberry, raspberry and strawberry fruit, making observation of the fruit colouring phenophase impractical; both the initial and final harvest dates are reported);
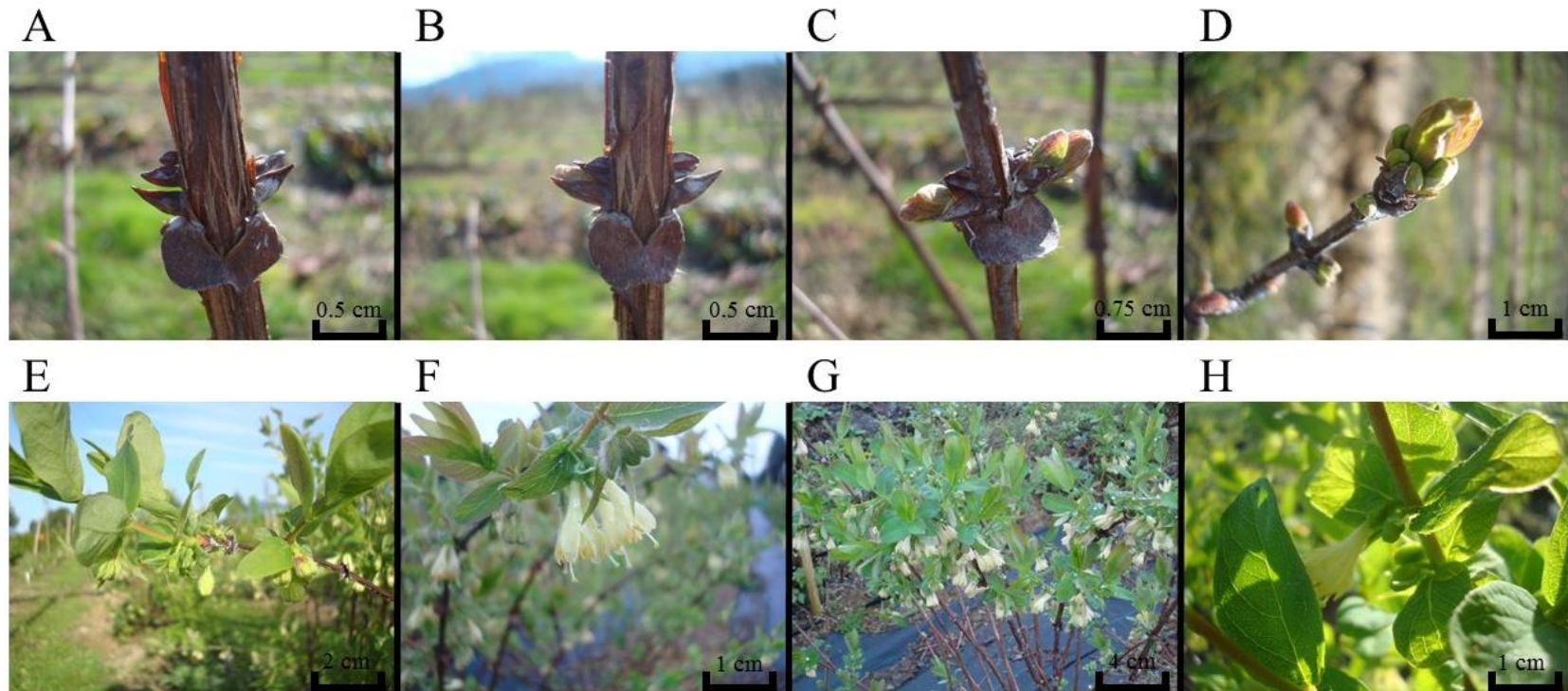
Figure 3.4. Blue honeysuckle phenological stages from plant dormancy to fruit set. (A) Dormant axillary buds on one-year-old stem (B) axillary bud with bud scales broken – bud break scored at 10%, 50% and 90% of buds achieving this stage (C) Newly emerging leaves from broken axillary buds (D) Flower pairs surrounding the newly emerging leaves and shoot of an apical bud (E) Newly emerged flowers just prior to opening (F) Fully open flower pairs on the first node of new growth and fully closed flowers on the next node – flowering onset scored at first open flower and at opening of 30% and 90% of first node flowers (G) Full bloom with vigorous new shoot growth following the flowering onset phenophase (H) Newly set fruit with petal fall underway.
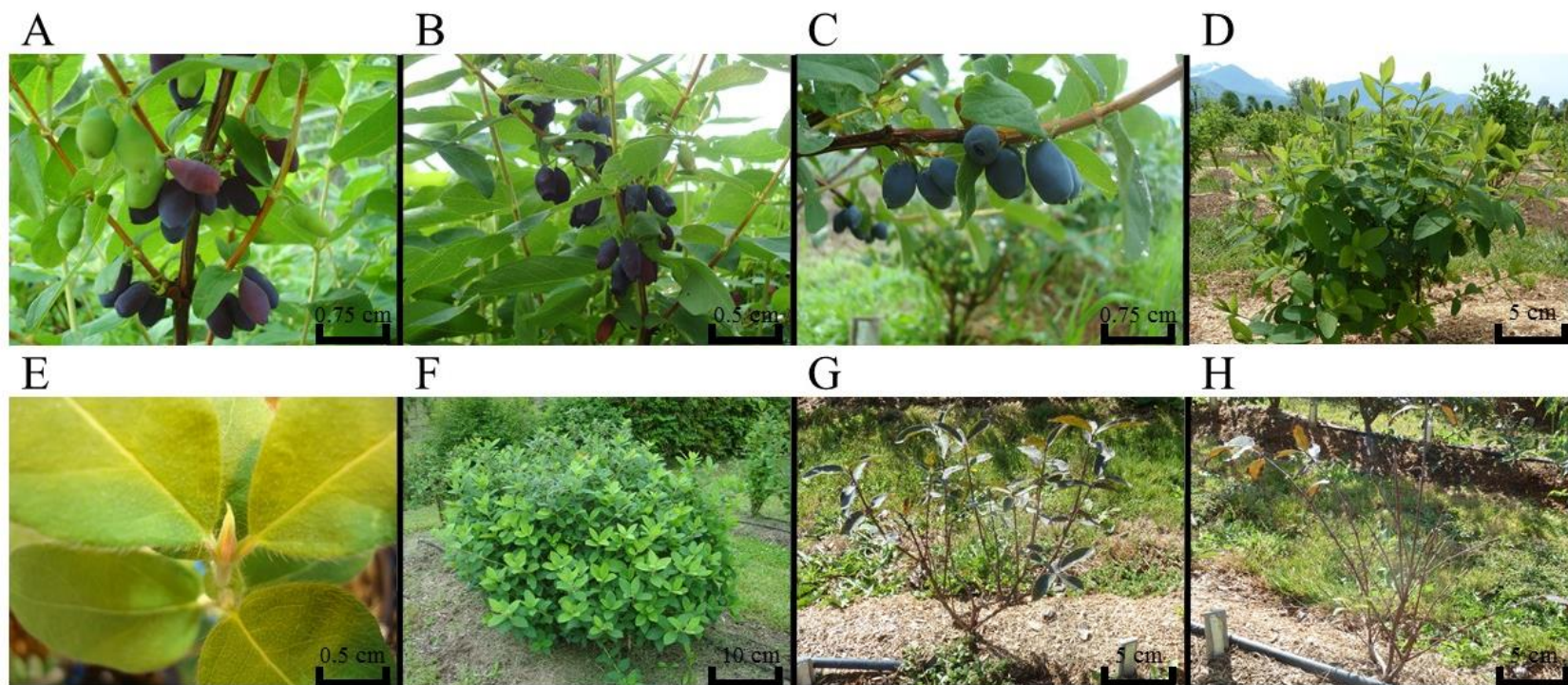
Figure 3.5. Blue honeysuckle phenological stages from fruit ripening to plant dormancy. (A) 50% blue fruit (B) 75% blue fruit (C) 100% blue fruit, which was followed by synchronous harvest of all fruit per plant three to five days later (D) Active shoot growth during early fruit development (E) Newly setting apical bud after spring growth (F) Vegetative growth cessation for an entire plant (G) 50% leaf drop (H) 95% leaf drop.

- Vegetative growth cessation was defined as the setting of a terminal bud on new shoots as the plant begins to prepare for dormancy (not recorded for comparison crops due to incomparable growth cycles); and

- Leaf drop was recorded at 50 and 95% of all leaves on each plant (not recorded for strawberry due to non-woody growth habit).

3.4 Morphological Measurements and Ratings

Morphological traits were measured from each individual plant in both sets of trials in 2012 and 2013 (equivalent to third and fourth years after planting compared to standard planting stock). Based on phenological observation, the entire harvest from each bush was used to determine fruit yield, average weight (25 fruit sample) and fruit length and width (three technical replicates). Subsequently, fruit length:width, length:weight and width:weight ratios were calculated. There were 18 biological replicates per genotype for the foundation germplasm trial (three blocks x three locations x two years). After averaging three technical replicate clones in each block, there were six biological replicates for the improved germplasm trial (three blocks x one location x two years).

Each sample was evaluated qualitatively for shape and agronomic potential. Inherent within-genotype and within-sample heterogeneity in shape was systematically characterized by rating primary ($1^°$) and secondary ($2^°$) shapes through visual inspection of each harvest *en masse* (**Figure 3.6**). $1^°$ shapes were scored when they represented more than one quarter of each harvest, and $2^°$ shapes were scored when they represented less than one quarter of a harvest or when they were observed in only a portion of biological replicates. Photographic documentation of each harvest was used to reconcile independent observations to determine an overall fruit shape combination for each genotype comprised of one or more $1^°$ and one or more $2^°$ ratings. Independently, the proximal and distal ends of the fruit were scored for $1^°$ and $2^°$ shapes as for the overall fruit shape.

Subsequently, sixteen categorical variables (**Table 3.4**) were rated by a single observer for their impact on agronomic potential: fruit synanthy without regard to the proportion of affected fruit (i.e., incomplete synanthy of a single fruit in an individual harvest yielded an 'incomplete' rating); evenness of fruit surface; degree of fruit pubescence; degree of waxy cuticle (i.e., bloom); fruit colour; fruit shape in cross-section; size of the opening at the distal fruit end; heterogeneity in fruit size; heterogeneity in fruit shape; severity of fruit mold; fruit flesh firmness; fruit taste
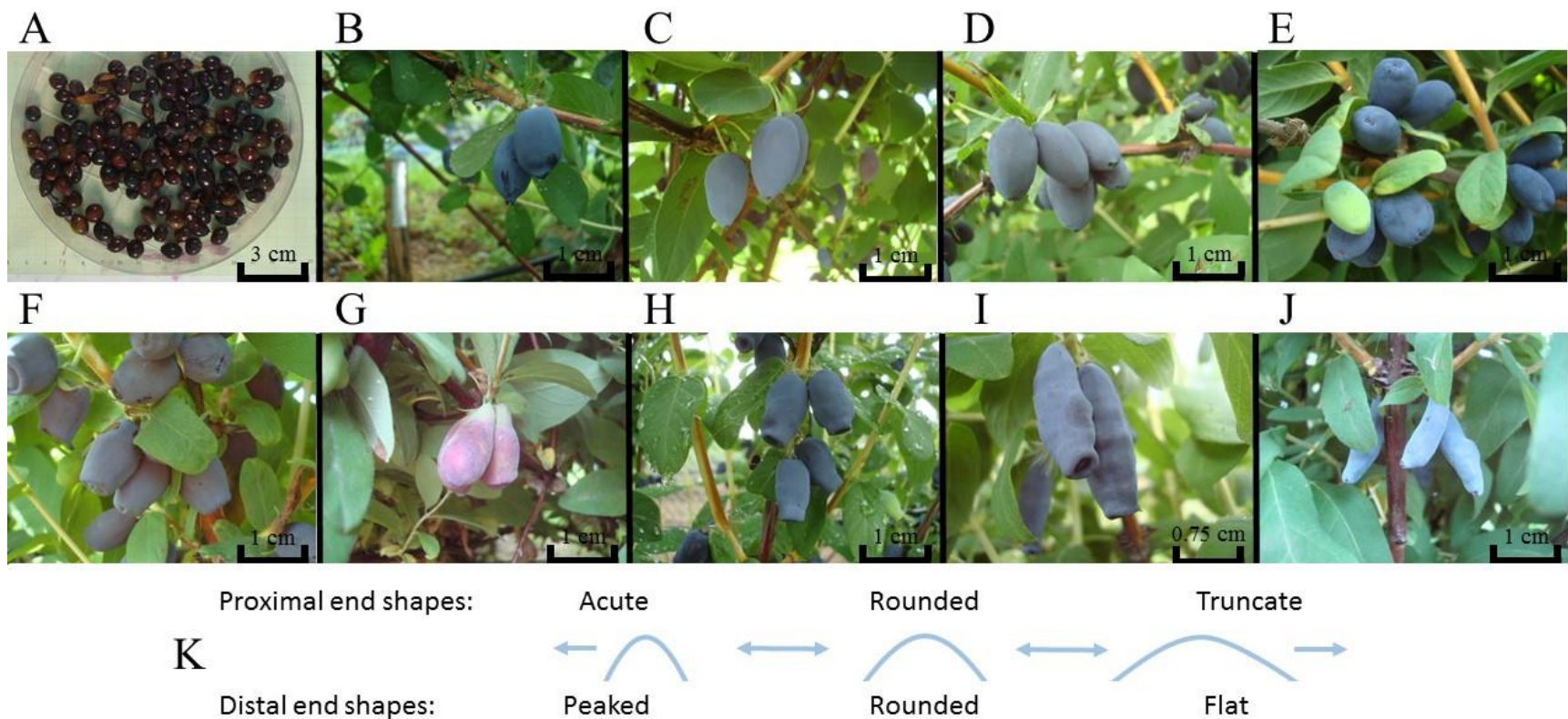
Figure 3.6. Blue honeysuckle overall fruit shapes and proximal and distal end shapes. (A) Round-shaped Canadian fruit (not included in current study) (B) Ovate-shaped Japanese fruit (C) Torpedo-shaped Japanese fruit (D) Oblong-shaped (i.e., oval) Japanese fruit (E) Cylindrical-shaped (i.e., elongated) Kuril fruit (F) Bell-shaped Japanese/Kuril fruit (G) Pear-shaped (i.e., obovate) Japanese/Russian fruit (not yet fully ripe) (H) Bottle-shaped Japanese fruit (I) Spindle-shaped Russian fruit (J) Pod-shaped Russian fruit (K) Proximal and distal fruit end shapes (additional indented distal end shapes not drawn, but can be seen in H and I).

Table 3.4. Categorical ratings for fruit traits related to agronomic potential in blue honeysuckle foundation and improved germplasm evaluated in the Fraser Valley, BC, Canada.

Variable	#	Rating	Variable	#	Rating
Fruit Synanthy	1	Complete		1	Dark blue
	2	Incomplete	Fruit Colour	2	Purplish-blue
Fruit Surface	1	Smooth		3	Bluish-purple
	2	Slightly bumpy		1	Circular
	3	Moderately bumpy	Fruit Shape in Cross Section	2	Broad elliptic or circular
	4	Bumpy		3	Broad elliptic
	5	Very bumpy		4	Narrow or broad elliptic
Fruit Pubescence	1	Absent		5	Narrow elliptic
	2	Minimal		1	Closed
	3	Very slight		2	Very small
	4	Slight		3	Small
	5	Moderately low	Fruit Opening Size	4	Medium-small
	6	Moderate		5	Medium
	7	Moderately high		6	Medium-large
	8	High		7	Large
	9	Very high		1	None
Fruit Bloom	1	Very heavy		2	Minimal
	2	Heavy	Fruit Mold	3	Moderate
	3	Moderately heavy		4	Severe
	4	Moderate		1	Minimal
	5	Dull	Heterogeneity of Fruit Size and Shape	2	Slight
	6	Very dull		3	Moderate
	7	Minimal		4	High
				5	Very high

Table 3.4. Continued. Categorical ratings for fruit traits related to agronomic potential in blue honeysuckle foundation and improved germplasm evaluated in the Fraser Valley, BC, Canada.

Variable	#	Rating	Variable	#	Rating
Fruit Taste	1	Sweet	Attachment Strength	1	Extremely loose
	2	Sourish-sweet		2	Very loose
	3	Sweetish-sour		3	Loose
	4	Sour		4	Moderately loose
	5	Very sour		5	Moderate
	6	Astringent		6	Moderately tight
Fruit Aroma	1	Very high		7	Tight
	2	High		8	Very tight
	3	Moderately high		9	Extremely tight
	4	Moderate	Stems in Fruit Harvest	1	None
	5	Slight		2	Very slight
	6	Very slight		3	Slight
	7	Minimal		4	Moderate
Fruit Flesh	1	Very firm		5	Moderately high
	2	Firm		6	High
	3	Doughy		7	Very high
	4	Doughy-soft			
	5	Soft			
	6	Very soft			
	7	Watery			
Fruit Scar	1	Small and dry			
	2	Small and wet			
	3	Large and dry			
	4	Large and wet			

(rankings for bitterness were not observed in the selected germplasm); fruit aroma; quality of the picking scar; retention of stems in harvested fruit; and strength of fruit attachment to the plant.

3.5 Biochemical Assays

After morphological characterization, refrigerated fruit were split into two sub-samples that were frozen within 24 h of harvest: the first (187.3 +/- 3.2 g SE) in a polypropylene bag and the second (48.0 +/- 0.2 g SE) in a 7.6 by 10.2 cm nylon mesh bag. As for phenological and morphological measures, each blue honeysuckle genotype had 18 (three blocks x three locations x two years) biological replicates for the foundation germplasm trial and six biological replicates (three blocks [with three pooled technical replicates] x two years) for the improved germplasm trial. Since the comparison crops were sub-sampled from several harvests, assays were conducted on pooled samples from the first three harvests from each plant, but with the same amount of biological replication as for the blue honeysuckle germplasm.

3.5.1 Determinations of Fruit Quality

After storage at -20°C, the first sub-sample was thawed at room temperature and homogenized in a food processing blender. Approximately 60 mL of fruit homogenate was centrifuged at 2,300x g in an Eppendorf Centrifuge 5810 R (Eppendorf North America, Hauppauge, NY, USA) for 5 min to obtain fruit juice supernatant for three biochemical assays related to fruit quality (FQ): 1) total soluble solids (TSS) (Marsh et al 2004) with two technical replicates, using a refractometer (Sper Scientific, Scottsdale, AZ); 2) titratable acidity (TA) with two technical replicates, using an HI84432 Automatic Fruit Juice titrator with built-in pH and temperature probes (Hanna Instruments Canada, Laval, QC, Canada), calculated in percent citric acid equivalents (CAE); and 3) pH using the titrator's pH probe without technical replication. For TA and pH, 2 mL aliquots of supernatant were diluted with 48 mL of distilled water and then automatically titrated with HI84432-50 titrant solution (Hanna Instruments Canada, Laval, QC, Canada). The pH electrode was 3-point calibrated and the titrant pump calibrated daily.

3.5.2 Determinations of Nutritional Content

After storage at -40°C, the second set of sub-samples was freeze-dried in a freeze dryer (Labconco Corp., Kansas City, MO, USA) for 168 h. After drying, each sample was pulverized,

weighed and stored in 14 mL polypropylene culture tubes (VWR International, Radnor, PA, USA) at -20$°$C until being used for three biochemical assays related to nutritional content: 1) Folin Ciocalteau (FC) assay for total phenolics (TP) (Kim et al 2003; Singleton et al 1999); 2) Trolox Equivalence Antioxidant Capacity (TAC) assay (Re et al 2000; Ghiselli et al 2000); and 3) Ferric Reducing Antioxidant Potential (FRAP) assay (Benzie and Strain 1996).

Approximately 100 mg powderized fruit samples were weighed out into 14 mL polypropylene tubes. The actual weight of each sample was used with the percent dry matter for that same sample used to calculate assay values on both a fresh weight (FW) and dry weight (DW) basis. Batches of 24 samples were dissolved in 4 mL acidified methanol (99.5% methanol 99:1 v/v with formic acid), vigorously mixed then sonicated for 10 min in a 35 kHz Ultrasonic Cleaner (VWR International, Radnor, PA, USA), centrifuged for 15 min at 800x g and decanted into a clean 50 mL tube. This was repeated three times for a final volume of 12 mL of methanolic extract. Working solutions were made by 8x dilution with acidified methanol into 2 mL tubes, after which they were refrigerated and assayed within 24 h. The stock solution for each standard curve (**Appendix A.4**) was frozen and new dilute solutions and standard curves were prepared daily. Using a Bio-Tek ELx800 Absorbance Reader (Bio-Tek Instruments, Winooski, VT, USA) and 96-well flat-bottom polystyrene microplates (Greiner Bio-One, Frickenhausen, Germany), three technical replicates of an eight-increment standard and batches of 24 samples were analyzed. Individual timers were used to coordinate the sequence of assays, while the different lengths of reaction times permitted simultaneous measurement on the same spectrophotometer by switching between wavelength filters. In this manner, a relatively high-throughput procedure was developed after a series of preliminary optimization experiments. The optimized procedure was used to analyze 96 samples in a period of 8 h. See **Appendix A.5** for complete list of chemicals.

For TP, a 100-1000 µM gallic acid (GA) standard was compared to 10 µL dilute samples mixed with 90 µL diH$_2$0 and 10 µL FC reagent and incubated in the dark at room temperature for 5 min. Addition of 100 µL sodium bicarbonate was followed by incubation for 90 min and measurement of absorbance at 750 nm.

For TAC, the 2,2′-azino-bis-(3-ethylbenzthiazoline-6-sulfonic acid) free radical (ABTS+) was diluted with acidified methanol to absorbance of 0.70 +/- 0.02 (47 µM). Compared to a 0.025-0.250 mM Trolox standard curve in dimethyl sulfoxide (DMSO), 30 µL samples were combined with 250 µL ABTS+ and absorbance measured at 734 nm after 5 and 15 min.

For FRAP, a 10:1:1 working solution of acetate buffer (pH 3.6), 10 mM 2,4,6-Trispyridyl-s-triazine (TPTZ) and 20 mM iron chloride was heated to 37°C. A standard curve of 100-1000 uM L-ascorbic acid was used to compare 10 µL samples mixed with 40 µL diH$_2$0 and 300 µL FRAP working solution with absorbance read at 593 nm after 4 and 14 min.

The three technical replicates on each microplate were used to calculate standard curves by subtracting the absorbance of the blank and producing an XY plot of concentration vs. absorption. Regression lines of best fit (R^2 > 0.98) were used to calculate the equivalent concentration based on the average of three technical replications for each sample and convert to the appropriate units: mg gallic acid equivalents (GAE)/100 g FW/DW for TP; mmol Trolox equivalents (TE)/100 g FW/DW for TAC; and mmol ascorbic acid equivalents (AAE)/100 g FW/DW for FRAP. Sample-specific FW/DW calculations and assay durations for TAC (5 and 15 min) and FRAP (4 and 14 min) were compared.

3.6 Statistical Analysis and Interpretation

3.6.1 Analysis of Quantitative Variables

The foundation germplasm trial and improved germplasm trial were described separately using summary statistics for each continuous phenological, morphological and biochemical variable. General trends were interpreted within and between blue honeysuckle groups and the comparison crops. Density plots were used to compare the distributions of observations for each improved group. Data were checked for normality and homoscedasticity, and only fruit yield required log transformation to conform to the latter assumption. Each variable was then analyzed using linear mixed model regression in the 'R' statistical environment (R Development Core Team 2015) using the 'lme4' package (Bates et al 2015). For the foundation germplasm trials, genotype was the sole fixed factor, whereas block, location and year were included as random factors. For the improved germplasm trial, block averages for each genotype were calculated from three independently-observed technical replicate clones and then block and year were treated as random factors. Linear contrasts were extracted from each mixed model and pairwise comparisons were made between each combination of genotypes using the 'multcompView' package (Graves et al 2015) to determine statistically significant differences (p<0.05). For the improved germplasm trial, the parent genotypes used to produce each family of four improved siblings were compared to categorize them as higher, lower or equivalent to one another. The improved genotypes were

compared to their parents for placement in one of five statistical categories (earlier or later for phenological traits; lower or higher for morphological or biochemical traits):

- Early/low transgressive segregant if significantly earlier/lower than both parents;

- Early/low-parent type if significantly earlier/lower than one parent but equivalent to the other;

- Intermediate type if not different from either parent or statistically earlier/lower than one and statistically later/higher than the other;

- Late/high-parent type if significantly later/higher than one parent but equivalent to the other;

- Late/high transgressive segregant if significantly later/higher than both parents.

The proportions of these categories were used to make general inference of mode of gene action in improved groups and compare combinations of foundation groups. For heritability analysis, broad-sense heritability (H^2) was calculated across the foundation and improved germplasms combined and separate and in each foundation and improved group individually by extraction of variance components from mixed models and division of genetic variance by total phenotypic variance ($H^2 = V_G/V_P$ where V_G is total genetic variance and V_P is total phenotypic variance). For narrow-sense heritability (h^2), the mid-parent value for each hybrid genotype was calculated and mid-parent regression applied using phenotypic averages (where h^2 is the slope of the regression line of mid-parent). Pearson's correlations were calculated for continuous variables and Rho correlations for categorical variables, using phenotypic averages in both cases. The degree of heritability and the strength of correlations were interpreted heuristically (**Appendix A.6**).

3.6.2 Analysis of Qualitative Variables

For the foundation germplasm trial, fruit shape as well as proximal and distal end shapes for each genotype were compared by tabular summarization. For the improved germplasm trial, the proportions of $1°$ and $2°$ shapes for each genetic group, rather than genotype, were compared. Associations between fruit shapes were compared across groups.

For both foundation and improved germplasm trials, the proportions of each categorical fruit morphological rating were compared across genetic group and numerical averages were tabulated for each genotype. In addition, for the improved germplasm trial, summary statistics were generated for each genetic group, while H^2 and h^2 were calculated as above. Using all categorical fruit morphological variables, a relative selection index (SI) was calculated. Each trait

was range standardized (0 to 1) to remove the effect of different numbers of categories between variables (i.e., a two-rating variable would have the same effect as a nine-rating variable), and the overall trait mean was subtracted from the value of the trait for each genotype. Summation of all trait scores permitted interpretation of trends between traits within and across groups.

$$I_{Rel} = b_1(x_1 - x_{1(avg)}) + b_2(x_2 - x_{2(avg)}) + b_3(x_3 - x_{3(avg)}) + \ldots + b_{16}(x_{16} - x_{16(avg)})$$

I_{Rel} is the index relative to each trait; x_1, x_2, x_3, to x_{16} are range standardized (0 to 1) fruit traits; x_{avg} is the trait average across all genotypes; b_1, b_2, b_3 to b_{16} are equal weightings (1).

4. CHAPTER 4: PHENOLOGICAL ADAPTATION OF BLUE HONEYSUCKLE GERMPLASM

4.1 Introduction

The northern limits of blue honeysuckle's native distribution are determined by insufficient heat during the summer, harsh frosts and infertile soils, whereas heat and drought set the southern limits to its range (Sheyko 2009). With general adaptation to cold, continental climates, suitability of blue honeysuckle for temperate climates is questionable due to low chilling requirement and early bud break during fluctuating winter temperatures (Plekhanova 1986). Breeding of blue honeysuckle cultivars with adaptation to temperate climates is important for expanding its range of production and facilitating its development as a large-scale commercial crop (Thompson 2006b). Key research objectives include determining genetic diversity for important traits related to phenological adaptation in three important foundation germplasm groups, the ability to make genetic progress in three improved germplasm groups and the physiological and genetic complexity of phenological adaptation. Therefore, to inform breeding strategies to expand climatic adaptation, phenological adaptation was evaluated for a broad range of blue honeysuckle germplasm compared to blueberry, raspberry and strawberry in a temperate climate in the Fraser Valley, British Columbia, Canada.

4.2 Results and Discussion

4.2.1   Spring Phenology of Foundation Germplasm

4.2.1.1 Description and Comparison of Foundation Germplasm Groups

At bud break, there was a slight overlap between the latest Russian and earliest Japanese genotypes and between the latest Japanese and earliest Kuril genotypes, but no overlap was observed between the latest Russian and earliest Kuril genotypes (**Figure 4.1**; **Table 4.1**). While first open flower was characterized by more distinct outliers than at any estimate of bud break the foundation groups were more tightly clustered for the rest of the flowering onset phenophase (**Table 4.2**) and for the fruit colouring/harvest phenophase (**Table 4.3**). Accompanying this pattern was an increase in the normality of distribution for the Japanese and Russian groups, whereas the Kuril group was characterized by four nearly identical phenotypes and one much earlier genotype (K-97-12). The phenological gap between the Japanese and Kuril groups narrowed from bud break to flowering onset and from flowering onset to fruit colouring/harvest,

Group or Crop	Feb. 10	Feb. 20	Mar. 1	Mar. 11	Mar. 21	Mar. 31	Apr. 10	Apr. 20	Apr. 30	May 10	May 20	May 30	Jun. 9	Jun. 19	Jun. 29	Jul. 9	Jul. 19	Jul. 29	Aug. 8	Aug. 18	Aug. 28
Japanese																					
Kuril																					
Russian																					
Blueberry																					
Raspberry																					
Strawberry																					
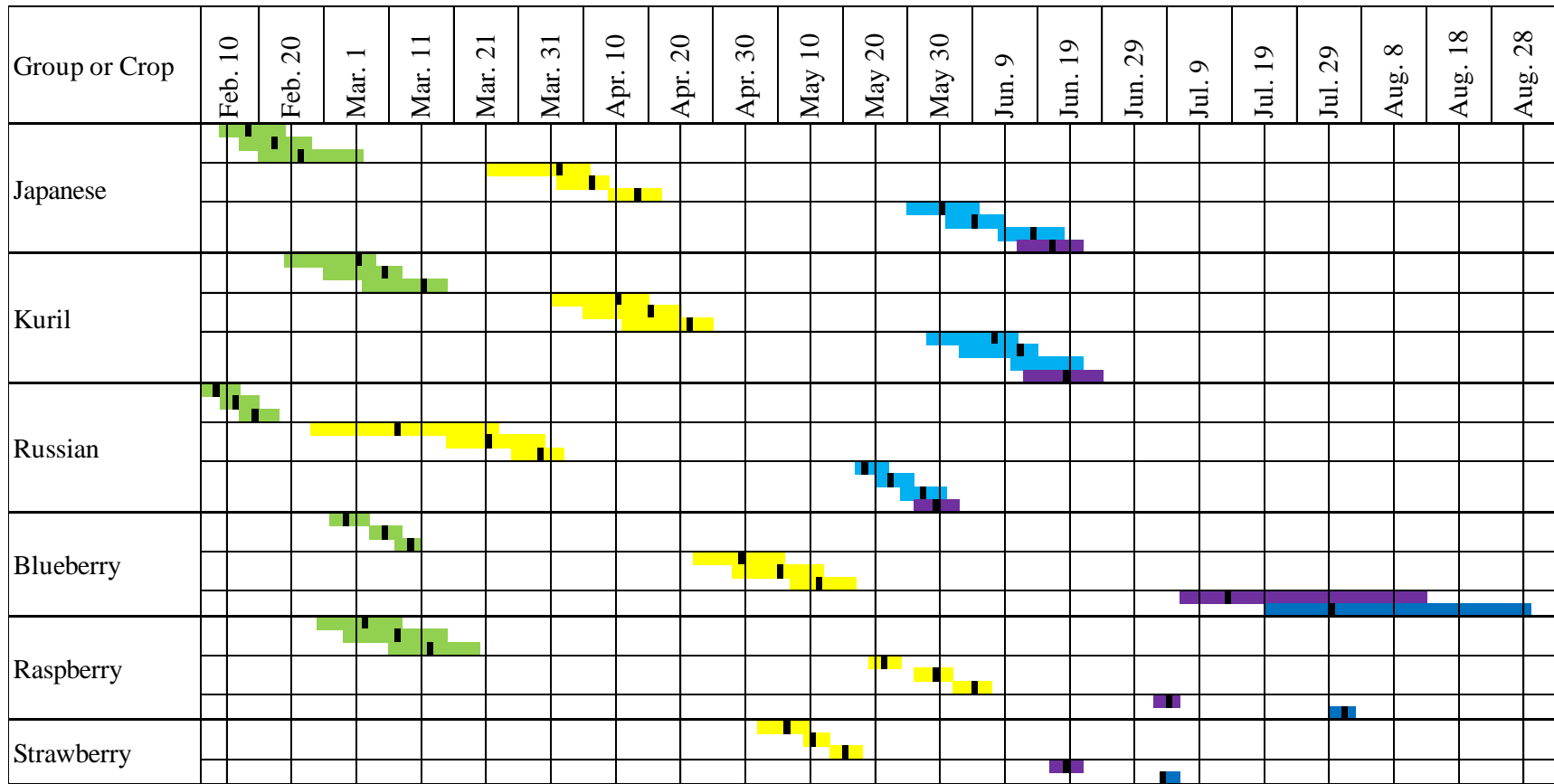
Figure 4.1. Foundation Germplasm: Spring phenological development in blue honeysuckle and comparison crops in 2012/2013 in the Fraser Valley, BC, Canada (bars represent the range of phenotypic averages for each group with the group average indicated by a black bar, ▮ – bud break (top – 10%, centre – 50%, bottom – 90%), ▮ – flowering onset (top – first open flower, centre – 30%, bottom – 90%), ▮ – fruit colouring (top – 50%, centre – 75%, bottom – 100%), ▮ – simultaneous blue honeysuckle and first comparison crop harvest, ▮ – final comparison crop harvest).

Table 4.1. Foundation Germplasm: Bud break phenophase in blue honeysuckle and comparison crops in 2012/2013 in the Fraser Valley, BC, Canada.

Group	Japanese	Kuril	Russian	Blueberry	Raspberry
10% Bud Break					
Average	Feb. 13	Mar. 1	Feb. 8	Feb. 28	Mar. 2
Median	Feb. 13	Mar. 3	Feb. 8	Feb. 27	Mar. 1
Earliest	Feb. 9	Feb. 19	Feb. 6	Feb. 26	Feb. 24
Latest	Feb. 18	Mar. 3	Feb. 11	Mar. 2	Mar. 7
Range (days)	8.6	12.4	5.1	4.3	11.7
50% Bud Break					
Average	Feb. 17	Mar. 5	Feb. 11	Mar. 5	Mar. 7
Median	Feb. 16	Mar. 7	Feb. 11	Mar. 4	Mar. 6
Earliest	Feb. 12	Feb. 25	Feb. 9	Mar. 3	Feb. 28
Latest	Feb. 23	Mar. 7	Feb. 14	Mar. 7	Mar. 14
Range (days)	11.1	10.7	5.2	3.5	13.8
90% Bud Break					
Average	Feb. 21	Mar. 11	Feb. 14	Mar. 9	Mar. 12
Median	Feb. 20	Mar. 13	Feb. 14	Mar. 9	Mar. 11
Earliest	Feb. 15	Mar. 2	Feb. 12	Mar. 7	Mar. 6
Latest	Mar. 1	Mar. 14	Feb. 17	Mar. 10	Mar. 19
Range (days)	13.2	11.6	5.2	3.2	13.8

Table 4.2. Foundation Germplasm: Flowering onset phenophase in blue honeysuckle and comparison crops in 2012/2013 in the Fraser Valley, BC, Canada.

Group	Japanese	Kuril	Russian	Blueberry	Raspberry	Strawberry
First Open Flower						
Average	Apr. 1	Apr. 10	Mar. 7	Apr. 29	May 21	May 6
Median	Apr. 2	Apr. 13	Mar. 7	Apr. 30	May 22	May 6
Earliest	Mar 21.	Mar. 31	Feb. 23	Apr. 22	May 19	May 2
Latest	Apr. 5	Apr. 14	Mar. 22	May 5	May 23	May 9
Range (days)	14.5	14.1	27.3	12.7	3.9	7.0
30% Flowering Onset						
Average	Apr. 6	Apr. 15	Mar. 21	May 5	May 29	May 10
Median	Apr. 6	Apr. 18	Mar. 21	May 6	May 29	May 10
Earliest	Apr. 1	Apr. 5	Mar. 15	Apr. 28	May 26	May 9
Latest	Apr. 8	Apr. 19	Mar. 29	May 11	May 31	May 12
Range (days)	7.1	13.6	13.8	13.4	4.6	3.6
90% Flowering Onset						
Average	Apr. 13	Apr. 21	Mar. 29	May 11	Jun. 4	May 15
Median	Apr. 14	Apr. 23	Mar. 29	May 11	Jun. 4	May 14
Earliest	Apr. 9	Apr. 11	Mar. 25	May 7	Jun. 1	May 13
Latest	Apr. 16	Apr. 24	Apr. 1	May 16	Jun. 6	May 17
Range (days)	6.4	13.1	7.6	9.1	4.7	3.3

Table 4.3. Foundation Germplasm: Fruit colouring and harvest phenophase in blue honeysuckle and comparison crops in 2012/2013 in the Fraser Valley, BC, Canada.

Group	Japanese	Kuril	Russian	Group	Japanese	Kuril	Russian
50% Blue Fruit				Sole Harvest (Blue Honeysuckle)			
Average	May 30	Jun. 7	May 18	Average	Jun. 16	Jun. 21	May 28
Median	May 30	Jun. 9	May 18	Median	Jun. 15	Jun. 22	May 27
Earliest	May 25	May 28	May 17	Earliest	Jun. 11	Jun. 12	May 26
Latest	Jun. 4	Jun. 10	May 21	Latest	Jun. 20	Jun. 23	Jun. 1
Range (days)	10.1	12.9	4.8	Range (days)	9.1	10.7	5.8

Group	Japanese	Kuril	Russian	Group	Blueberry	Raspberry	Strawberry
75% Blue Fruit				First Harvest (Comparison Crops)			
Average	Jun. 4	Jun. 11	May 22	Average	Jul. 19	Jul. 4	Jun. 18
Median	Jun. 4	Jun. 13	May 21	Median	Jul. 13	Jul. 4	Jun. 18
Earliest	May 31	Jun. 2	May 20	Earliest	Jul. 7	Jul. 2	Jun. 16
Latest	Jun. 8	Jun. 13	May 25	Latest	Aug. 12	Jul. 5	Jun. 20
Range (days)	8.4	11.1	5.2	Range (days)	35.5	2.1	4.2

Group	Japanese	Kuril	Russian	Group	Blueberry	Raspberry	Strawberry
100% Blue Fruit				Final Harvest (Comparison Crops)			
Average	Jun. 13	Jun. 18	May 26	Average	Jul. 29	Jul. 31	Jul. 3
Median	Jun. 13	Jun. 20	May 25	Median	Jul. 26	Jul. 31	Jul. 3
Earliest	Jun. 9	Jun. 10	May 24	Earliest	Jul. 19	Jul. 29	Jul. 3
Latest	Jun. 17	Jun. 20	May 30	Latest	Aug. 28	Aug. 1	Jul. 5
Range (days)	8.7	9.8	6.7	Range (days)	40.0	2.8	2.4

which increased the overlap between these groups as the season progressed. In contrast, the phenological distance between the Japanese and Russian groups was greater at flowering onset than at bud break, and it was even greater by the end of fruit colouring/harvest.

For the early Russian group at bud break, R-27-35 was significantly later than all other Russian genotypes and statistically equivalent to most of the Japanese group (**Appendix B.1**). There were few statistical differences between the remaining Russian genotypes, but there was sufficient range within the Japanese group for differences to be detected between genotypes. By first open flower, the only overlap between the Japanese and Russian groups resulted from the inclusion of R-27-35 (later than all other Russian genotypes) and J-45-14 (earlier than all other Japanese genotypes) (**Appendix B.2**). At 30% flowering onset, R-27-35 was no longer as late as any of the Japanese genotypes and, at 90%, was not significantly earlier than the rest of the Russian group. The distance between the Japanese and Russian groups increased over the fruit colouring/harvest phenophase as the range of responses within these groups normalized (**Appendix B.3**).

On the late end of the spectrum, though statistically equivalent to the latest Japanese genotypes at bud break, K-97-12 was significantly earlier than the four other Kuril genotypes, which were not different from one another. The overlap between the Japanese and Kuril groups was greater at flowering onset than at bud break, a shift that continued through fruit colouring/harvest. Specifically, K-97-12 was statistically earlier than the latest Japanese genotypes at flowering onset, intermediate to the earliest and latest at fruit colouring and equivalent to the earliest at harvest.

R-27-35 and K-97-12 overlapped the intermediate Japanese group and were clear Russian and Kuril outliers, respectively, with more moderate phenology overall. This is explained by their genetic heritages, each suspected to have a minority of the opposing group in its pedigree. Also, the early Japanese outlier (J-45-14) had relatively inconsistent bud break, leading to early, uneven opening of its first flowers.

Compared with reports from the colder climates of Japan and Russia, spring phenology is much earlier in the Fraser Valley's temperate climate, which is attributed to a high number of chill hours and warm winter conditions that permit earlier bud break. No literature sources quantify phenology in the Kuril germplasm and reports on Japanese and Russian germplasm are comparatively incomplete as they address only one foundation group or the other. In Hokkaido

(*Dfb*), descriptions of the sole registered cultivar, 'Yufutsu', which is a relatively early *emphyllocalyx* representative, indicate bud break in mid-April, flowering onset in mid-May, fruit colouring in late June and a prolonged harvest from the beginning to end of July (Tanaka et al 1994; Nakajima 1996). In the Fraser Valley, the Japanese germplasm reaches bud break two months earlier, flowering onset one and a half months earlier and fruit colouring one month earlier. A single, simultaneous harvest occurs two weeks before the start, and one and a half months before the end, of the same phenophase in Japan.

Russian sources report the phenology of *kamtschatica* germplasm across a range of continental climates in Eurasia (**Table 4.4**). The relative rate at which phenology advances in these regions compared variably to the Fraser Valley, with different regions advancing between phenophases relatively faster or slower, which suggests genotype x environment interactions. Compared to these colder climates, Russian blue honeysuckle in the Fraser Valley reaches bud break one to two and a half months earlier, flowering onset one to three months earlier and fruit colouring one week to one month earlier.

Despite some overlap between the latest Russian and earliest Japanese genotypes, and between the latest Japanese and earliest Kuril genotypes, germplasm group membership is the principal feature of phenological diversity across the foundation germplasm in the Fraser Valley. This elementary finding confirms qualitative observations in an even warmer climate in Corvallis, Oregon (Thompson and Barney 2007) and in a much colder environment in Saskatoon, Canada (Bors et al 2012). It is inferred that hybridization of these foundation groups is the best strategy for achieving new ranges in spring phenological adaptation, but crossing within each foundation group is the best means of maintaining a phenological range.

The Kuril group had a narrow range of phenological responses to the target environment, whereas the Russian group had a slightly broader and the Japanese group a considerably broader range. These differences in within-group variability confirm initial subjective observations of heterogeneity during germplasm evaluations at the U of S (Bors et al 2012), which led to selection of a greater number of Japanese than Russian genotypes and more Russian than Kuril genotypes for evaluation in the current study. The higher degree of variability in the Japanese group suggests a broad genetic base despite a more geographically concentrated provenance than the Russian material. The narrow range in adaptation for the Kuril group provides supporting evidence that the Kuril genotypes can be traced to a single clone sampled from Iterup Island. Therefore,

56

Table 4.4. Spring phenology in Russian blue honeysuckle from a range of regions in Russia.

Location	Bud Break	Flowering	Fruit Colouring	Reference
Pavlovsk (60° N)	Mar. 25-Apr. 10	May 5-15	Jun. 7-28	Plekhanova 2000
Komi Republic (64° N)	Apr. 27-29	End of May	Jun. 24-28	Ryabinina 2009
Kaluga oblast (54° N)	Mar. 15	Apr. 22-May 8	End of May	Esichev 2009
Primorye oblast (43° N)	Apr. 24	Mid-May	Mid-June	Stepanov 2009
Tomskaya oblast (59° N)	Apr.-May	End of May	End of June	Suchkova and Senina 2009
Mari El Republic (56° N)	Apr. 16-19	May 1-15	Jun. 8-19	Goluvunin 2009

accessing genetic variability for spring phenological adaptation to a temperate climate will be most successful using the Japanese group and, to a lesser extent, the Russian. Little variability is found in the Kuril group, suggesting a less useful source of within-group variability for breeding purposes. Since global variability in Japanese and Russian germplasm is broader than that represented in the current study, there is a high probability of making rapid genetic progress with these groups. In addition, crossing all three foundation groups presents an opportunity to generate novel phenotypes with superior adaptation to temperate climates (**Section 4.2.2**).

Shifts in the phenological distinctness between groups over the course of the spring phenophases suggest differences between these foundation groups in the underlying physiological control of phenological processes. Overall, distinctions between groups were greatest at bud break, less pronounced at flowering onset and even less so at fruit colouring/harvest. Between-group distinctness was greatest at bud break because the commencement of this phenophase is driven by the dual processes of chilling requirement satisfaction and accumulation of growing degrees. This implies important differences between these groups in both dormant-season and growing-season adaptive responses. The phenological distance increased between the Japanese and Russian groups, while it decreased between the Japanese and Kuril groups. Concurrently, the distribution within the Japanese and Russian groups normalized and the early Kuril outlier remained distinct from the cluster of four later genotypes. Between bud break and flowering onset, the distinctness between Japanese and Kuril groups was greatly diminished, indicating that it took a greater number of days for the latest Japanese genotype to pass from bud break to flowering onset than the earliest Kuril genotype. This cannot be interpreted simply because the timing of bud break sets a genotype-specific start date for subsequent accumulation of growing degrees, which is the principal driver of the progression through flowering onset and fruit colouring/harvest (Prischepina 2000). Therefore, each genotype progresses from phenophase to phenophase under a different set of daily average temperatures, meaning that cumulative growing degree sums are more comparable across germplasm groups than simply the number of days between phenophases. To illustrate, the distinctness between the Russian and Japanese groups remained relatively consistent, demonstrating that the former of these groups had a lower number of accumulated growing degrees or a lower base growing temperature, for the former group (unpublished data). The existence of genetic variability in the underlying physiological responses to a temperate

58

climate is evidence of the potential to leverage existing genetic resources to enhance adaptation to such environments (unpublished data).

For bud break, the extremely early phenology in the Russian foundation group is not a barrier to breeding for adaptation to a temperate climate *per se*, but the underlying cause of this early bud break results indirectly in fundamental maladaptation. Blue honeysuckle is known for its extreme winter and frost hardiness (Plekhanova 1989), but early bud break in the Russian foundation group is associated with low chilling requirement (Sarja 1998), which can lead to bud growth and secondary flowering in late fall or early winter in high chill environments (Kirin 2010). Fluctuating temperatures prevent newly broken buds from developing, exhausting carbohydrate reserves so that buds lose their ability to survive subsequent cold spells (Plekhanova 1989). In this study, the Russian material typically demonstrated die-back on the previous season's growth, leading to weak development in the following year and contributing to poor yields (**Section 5.2.1**). This confirms observations in Corvallis (Thompson and Barney 2007). Therefore, early-season fruiting is one of the desirable features of the crop, but extremely early Russian phenology and cold climate adaptation limit temperate climate adaptation indirectly and paradoxically through winter damage.

Temperate climate adaptation for the early blooming Russian (and some Japanese) germplasm is not limited by frost damage but by low levels of pollinator activity at that time of the season. Blue honeysuckle flowers are frost-resistant to -8°C (Plekhanova 1989), but blooming when honeybee activity is low will limit use of this germplasm in some temperate climates because native pollinators, that fly at lower temperatures, cannot be relied upon for large-scale horticultural production. Nonetheless, in the current study, the Russian germplasm, bloomed as early as the end of February and still set a small amount of fruit when no commercial honeybees were actively foraging. This is explained based on field observations of native pollinators (e.g., *Bombus* spp. and syrphid flies); a low requirement for viable seeds to initiate fruit development and some degree of parthenocarpy (as in highbush blueberry); a "leaky" self-incompatibility system (as in Solanaceous crops); or small amounts of wind pollination (as in cranberry). In fact, a high degree of self-fertility was documented in the Japanese cultivar, 'Yufutsu' (Nakajima 1996), and in Russian germplasm in controlled experiments (Plekhanova 1989). Consequently, though direct frost damage to flowers is not an adaptational constraint for early blue honeysuckle germplasm in temperate climates, inactivity of commercial honeybees is a limitation to maximum production.

59

4.2.1.2 Blueberry, Raspberry and Strawberry Compared to Foundation Germplasm

The absolute phenotypic range for the three estimates of bud break was five days for the Russian group and approximately ten days for the Kuril and Japanese groups (**Figure 4.1**; **Table 4.1**). In comparison, the blueberry cultivars reached each estimate of bud break over a span of three or four days, whereas the raspberry cultivars were spread over twelve to fourteen days.

Blueberry bud break was later than all Japanese and Russian genotypes as well as K-97-12 (**Appendix B.1**). In contrast, they were earlier or at the same time as the four late Kuril genotypes, depending on the cultivar and the specific estimate of bud break. Similarly, the raspberry cultivars reached 10% and 50% bud break earlier ('Saanich'), at the same time ('Cascade Bounty' and 'Chemainus') and later ('Meeker') than the four late Kuril genotypes. At 90% bud break, both 'Saanich' and 'Chemainus' were earlier than the four late Kuril genotypes. Across the phenophase, no raspberry cultivar broke bud as early as K-97-12 or any of the Japanese or Russian genotypes.

Opposite to bud break, the absolute phenotypic range for first open flower was a lengthy four weeks for the Russian group and half as broad for the Japanese and Kuril groups (**Table 4.2**). For 30% flowering onset, the Kuril and Russian groups varied by just under two weeks and the Japanese group by approximately one week. By 90% flowering onset, the Kuril group was still spread across two weeks, but the Russian and Japanese groups were each concentrated over one week.

In comparison, the blueberry cultivars reached first open flower and 30% flowering onset over approximately thirteen days, but they required only nine days at 90% flowering onset. The raspberry cultivars reached all three estimates of flowering onset within four or five days. The strawberry cultivars reached first open flower over a span of a week and 30% and 90% flowering onset in just over three days. The blueberries reached first open flower significantly later than the latest blue honeysuckle and the raspberries were later still. The strawberries reached flowering onset later than all blue honeysuckle and were intermediate between the blueberries and raspberries, overlapping with the former and being statistically distinct from the latter.

The Russian group reached 50% blue fruit over five days, whereas ten and thirteen days were required for the Japanese and Kuril groups, respectively (**Table 4.3**). These relative differences were similar for 75% blue and 100% blue fruit, narrowing over the course of the phenophase to one week for the Russian group and to nine and ten days for the Japanese and Kuril groups, respectively. The range in harvest dates mirrored observations at 100% blue fruit. The

60

four blueberry cultivars reached first harvest over a very long five-week period. In sharp contrast, the raspberry and strawberry cultivars reached initial harvest over two and four day spans, respectively. Correspondingly, the blueberry cultivars reached final harvest over a spread of 40 days, and the raspberry and strawberry cultivars finished within three days of each other.

At harvest, the blueberries and raspberries were far later than any blue honeysuckle (**Appendix B.2**). In contrast, the strawberries had significantly later harvest than the Russian group but were earlier than the four late Kuril genotypes. They were equivalent to several of the average Japanese genotypes, but were statistically intermediate to the earliest and latest in this group. All four strawberry cultivars were harvested until just after the latest Kuril genotype.

Full bloom following within a few days of 90% flowering onset and depending on daily temperatures, the Japanese and Kuril groups entered bloom when the ten-day average daily temperature was 8.9°C ($15.8/3.5^{\circ}$C maximum/minimum), while the following ten days averaged 11°C ($18.0/4.8^{\circ}$C maximum/minimum) (**Appendix B.4**; **Appendix B.5**; **Appendix B.6**). At these temperatures, honeybee activity is restricted to the warmest hours of the day but is sufficient to set blue honeysuckle fruit with an adequate supply of hives to supplement native pollinators. For the Russian group, average daily temperature was only 7.4°C ($15.4/0.9^{\circ}$C) with the following ten days averaging 9.2°C ($16.1/3.6^{\circ}$C). Combined with humid (**Appendix B.7**), rainy, windy conditions typical of this time of year in the Fraser Valley, pollination is highly restricted, as evidenced by poor fruit set in most Russian genotypes. In comparison, the blueberries and strawberries entered bloom with much warmer average temperatures of 14.5°C ($22.7/6.9^{\circ}$C) succeeded by a ten-day average of 13.1°C ($18.7/8.4^{\circ}$C), while the raspberries entered bloom with average temperatures of 14.2°C ($19.9/8.5^{\circ}$C) followed by 14.9°C ($20.1/9.4^{\circ}$C). Therefore, blue honeysuckle foundation germplasm has marginal adaptation to the Fraser Valley's temperate climate compared to blueberry, raspberry and strawberry as bloom occurs during sufficiently warm temperatures for the Japanese and Kuril groups but not the Russian group.

Compared to blueberry and raspberry, the earlier spring phenology in the Russian and Japanese groups starts with earlier bud break, which is based on a lower chilling requirement, lower base growing temperature or lower cumulative growing degree sum requirement for buds to open. Similar bud break phenology between the blueberries, raspberries and Kuril genotypes suggests similarity in these underlying physiological responses to the environment at the start of the season. Subsequently, flowering onset was considerably earlier for the Kuril group than for

the comparison crops, due to a very rapid progression from bud break to bloom for blue honeysuckle that is based on anatomical differences between crops. While blue honeysuckle fruit are produced from mixed buds, blueberry has separate floral and vegetative buds. The Kuril group required three weeks less time to progress from bud break to bloom than blueberry, which is evidence that blue honeysuckle has a faster rate of floral development under a similar temperature regime (i.e., lower cumulative growing degree requirement). Raspberry has mixed buds like blue honeysuckle, but lateral extension proceeds for a prolonged period during spring development preceding acropetalous bloom. This contrasts with basipetal bloom on new blue honeysuckle shoots. The Kuril group requiring six to seven weeks less time to pass from bud break to bloom compared with raspberry is directly related to this difference in flowering pattern.

Comparing the time between bloom and harvest, fruit development occurs more rapidly in strawberry than blue honeysuckle, evidenced by the later strawberry bloom followed by considerable overlap at harvest (**Figure 4.1**). To a lesser extent, raspberry's faster pace of fruit development results in a harvest phenophase that begins only slightly later than blue honeysuckle. In contrast, blueberry's much slower progression from bloom through fruit development results in a much later harvest phenophase than blue honeysuckle. Blue honeysuckle was considerably earlier than all three comparison crops at bloom, the Japanese, Kuril and Russian groups reaching 90% flowering onset 28, 20 and 43 days before the blueberry average; 52, 44 and 67 days before the raspberry average; and 32, 24 and 47 days before the strawberry average. Similarly, harvest was achieved 33, 28 and 52 days earlier than the blueberry average and 18, 10 and 37 days earlier than the raspberry average. Even though conditions during blueberry fruit development were warmer than for blue honeysuckle, the former took many more days to reach harvest. Raspberry fruit development took considerably fewer days than for blue honeysuckle, but development was not sufficiently quicker to result in simultaneity of harvest. In contrast, first harvest for strawberry averaged two and twenty-one days later than the Japanese and Russian groups, respectively, but three days earlier than the Kuril group, indicating a much faster development that results in overlap with blue honeysuckle's harvest phenophase.

From these comparisons, blue honeysuckle's relatively early phenology is related to different aspects of its phenological progression, depending on the crop to which it is compared. Compared to blueberry, blue honeysuckle's early-season fruiting is explained by earlier bud break and quicker progression from bud break to bloom and bloom to harvest, despite cooler

temperatures at the time of these phenological events. Compared to raspberry, most blue honeysuckle genotypes reach bud break earlier and progress to bloom much quicker at lower average temperatures, but fruit development in raspberry takes less time, resulting in a harvest phenophase that is closer to that of blue honeysuckle than at bloom. Strawberry's later bloom is counteracted by yet far quicker fruit development, resulting in substantial overlap in harvest with blue honeysuckle.

Overall, the Kuril group had similar bud break phenology to blueberry and raspberry, whereas the Japanese group sustained little to no damage despite its slightly earlier bud break. The Japanese and Kuril groups bloomed earlier than the three comparison crops, but pollinator activity was sufficient under the conditions of the current study to facilitate adequate pollination and fruit set. In contrast, the Russian group demonstrated limited adaptation to temperate climates because of its extremely early bud break and bloom.

4.2.1.3 Out-group Comparisons to Foundation Germplasm

For 10% and 50% bud break, J-PP was statistically the same as the earliest Japanese and latest Russian genotypes (**Appendix B.1**). The University of Saskatchewan (U of S) cultivars were also intermediate between the Russian and Japanese groups, and were not significantly different from the latest and earliest genotypes, respectively. At 90% bud break, the U of S cultivars were later than all Russian genotypes except R-27-35, while only 'Tundra' was later than J-PP.

J-PP was statistically the same as the early Japanese outlier (J-45-14) at first open flower; J-45-14, R-27-35 and 'Tundra' at 30% flowering onset; and intermediate between the Japanese and Russian groups, equivalent to only R-27-35, at 90% flowering onset. At first open flower and 30% flowering onset, 'Indigo Gem' was significantly earlier than R-27-35 and all Kuril and Japanese genotypes, while it was only as early as one other Russian genotype. At 90% flowering onset, 'Indigo Gem' was not earlier than R-27-35. At first open flower, 'Tundra' was the same as R-27-35 and J-45-14 but later than all other Russian genotypes and earlier than all other Japanese genotypes. At 30% flowering onset, 'Tundra' was earlier than all Japanese and Kuril genotypes. At 90% flowering onset, 'Tundra' was later than all but R-27-35 in the Russian group. At first open flower, 'Borealis' was later than all Russian genotypes as well as J-45-14 but was statistically the same as several average Japanese genotypes and K-97-12. At 30% flowering onset, 'Borealis'

was later than all Russian genotypes but statistically equivalent to some Japanese genotypes. At 90% flowering onset, 'Borealis' was later than all Russian genotypes. 'Indigo Gem' was earlier than the other two cultivars at first open flower and 30% flowering onset but not earlier than 'Tundra' at 90% flowering onset. In contrast, 'Borealis' and 'Tundra' were not different from one another at first open flower, but 'Tundra' was earlier than 'Borealis' at 30% and 90% flowering onset.

For each estimate of fruit colouring/harvest, J-PP was statistically earlier than the entire Japanese group and statistically equivalent to R-27-35 and R-2-16 (**Appendix B.2**). Across the phenophase, 'Borealis' was significantly later than all Russian genotypes, J-PP and the other U of S cultivars but earlier than all other Japanese and Kuril genotypes, except for J-45-14 at 50% blue fruit. At 50% blue fruit, 'Tundra' and 'Indigo Gem' were earlier than J-PP, R-27-35 and all Japanese and Kuril genotypes though statistically the same as most of the Russian group. For the rest of the phenophase, they were earlier than only the Japanese and Kuril genotypes and statistically the same as J-PP, R-27-35 and some other Russian genotypes.

The relatively early phenology of the U of S cultivars compared to the Kuril group, and their greater similarity to the Russian group may suggest dominance of early phenology, but basic observations of growth habit (i.e., shoot density, thickness and branching angle) demonstrate a lack of correlation with phenology. 'Indigo Gem' was slightly earlier but has similar morphology to the later Kuril parent. 'Borealis' was slightly later and bears morphological similarities to the early Russian group. 'Tundra' resembles 'Indigo Gem' but is more intermediate in phenology. Without knowing the proportion of Kuril genetics present in K-97-12 or the precise phenological response of the male parent (i.e., Blue Belle™), these are only preliminary indications of genetic dominance of early phenology and a lack of correlation between phenology and general growth habit.

Compared with the Japanese and Kuril groups, J-PP and the U of S cultivars bloomed during sub-optimal pollination and fruit set conditions in the Fraser Valley, as did the latest Russian genotypes. The limitations of these four genotypes are not as severe as the maladaptation seen for most Russian genotypes, which have low yields of small fruit with inconsistent size and shape indicative of inadequate seed set (**Section 5.2.1**). Also, fruit colouring in these genotypes overlapped with the later Russian genotypes but was significantly earlier than for the Japanese and Kuril groups. J-PP's phenology demonstrates the existence of a broader phenological range for

ssp. *emphyllocalyx* than sampled from the selective breeding program in Corvallis, from which the initial Japanese germplasm at the U of S was sourced. Similarly, ssp. *kamtschatica* is the primary representative in the Russian germplasm used in this study, but much earlier genetics exist within Russian germplasm globally (i.e., ssp. *edulis*, *altaica* and *pallasii).* Nonetheless, the utility of this additional genetic material is questionable (Plekhanova 1994a). Even the later range of Russian germplasm, ssp. *kamtschatica,* presents a major barrier to temperate climate adaptation, and earlier ranges in Japanese genetics may also be problematic. Therefore, use of Russian germplasm in breeding for temperate climates for introgression of desirable agronomic traits should employ selection against early phenology, which may necessitate breeding under controlled conditions. As evidenced by the limited adaptation of the three U of S cultivars to the Fraser Valley, selection of improved germplasm would benefit from evaluation in temperate climates before release as cultivars. Although phenological adaptation of Japanese and Kuril germplasm is acceptable under a temperate climate, selection against the earliest range of flowering onset in the Japanese group is advised to assure optimal pollination conditions in high chill environments.

4.2.2   Vegetative Growth Cessation and Leaf Drop of Foundation Germplasm
4.2.2.1 Description and Comparison of Foundation Germplasm Groups

The differences between genetic groups were far less distinct for growth cessation and leaf drop than for the spring phenophases described above (**Figure 4.2**; **Table 4.5**). The same general trend was observed, the Russian group reaching growth cessation earlier than the Japanese group, which was earlier than the Kuril group but with considerable overlap. For 50% leaf drop, the Russian group remained the earliest, but the Japanese and Kuril groups completely overlapped. The Russian group overlapped portions of both the Japanese and Kuril groups. For 95% leaf drop, the Russian group was distinctly earlier than the Japanese and Kuril groups, which overlapped one another as for 50% leaf drop.

R-27-35 stopped growing significantly later than all other Russian genotypes and was equivalent to several Japanese genotypes, including several that did not overlap for either flowering onset and fruit colouring (**Appendix B.8**). Two early Japanese genotypes from Bibai (J-21-78 and J-22-14) and a genotype crossed between material from Bibai and Chitose (J-73-39) were statistically different from the rest of the genotypes that were equivalent to some of the Kuril genotypes. The entire Kuril group reached growth cessation simultaneously, which was later than

65

Group or Crop	May 20	May 30	Jun. 9		Sept. 7	Sept. 17	Sept. 27	Oct. 7	Oct. 17	Oct. 27	Nov. 6	Nov. 16	Nov. 26	Dec. 6
Japanese														
Kuril														
Russian														
Blueberry														
Raspberry														
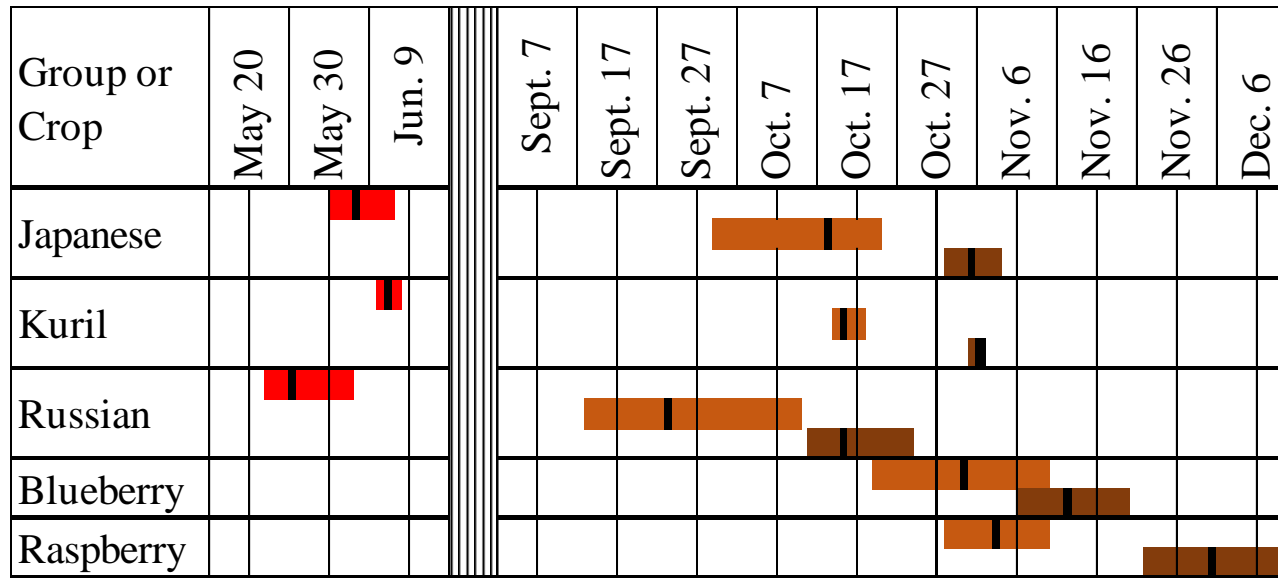
Figure 4.2. Foundation Germplasm: Vegetative growth cessation and leaf drop phenology in blue honeysuckle and comparison crops in 2012/2013 in the Fraser Valley, BC, Canada (bars represent the range of phenotypic averages for each group with the group average indicated by a black bar, ■ – vegetative growth cessation (end of major flush of early season growth), ■ – 50% leaf drop, ■ – 95% leaf drop).

Table 4.5. Foundation Germplasm: Vegetative growth cessation and leaf drop phenophases in blue honeysuckle and comparison crops in 2012/2013 in the Fraser Valley, BC, Canada.

Group	Japanese	Kuril	Russian	Group	Japanese	Kuril	Russian	Blueberry	Raspberry
	Growth Cessation				50% Leaf Drop				
Average	Jun. 2	Jun. 5	May 24	Average	Oct. 13	Oct. 14	Sept. 22	Oct. 29	Nov. 2
Median	Jun. 2	Jun. 5	May 23	Median	Oct. 12	Oct. 14	Sept. 21	Oct. 30	Nov. 3
Earliest	May 30	Jun. 4	May 21	Earliest	Sept. 29	Oct. 13	Sept. 12	Oct. 18	Oct. 27
Latest	Jun. 6	Jun. 6	May 31	Latest	Oct. 19	Oct. 16	Oct. 8	Nov. 8	Nov. 8
Range (days)	6.3	1.8	10.1	Range (days)	19.8	3.4	26.1	20.9	11.4
					95% Leaf Drop				
				Average	Oct. 31	Oct. 30	Oct. 14	Nov. 11	Nov. 29
				Median	Oct. 31	Oct. 30	Oct. 13	Nov. 11	Nov. 27
				Earliest	Oct. 28	Oct. 30	Oct. 10	Nov. 5	Nov. 21
				Latest	Nov. 3	Oct. 31	Oct. 22	Nov. 18	Dec. 7
				Range (days)	6.2	1.2	12.7	11.2	15.9

for the three earliest Japanese genotypes.

The Russian group showed a relatively normal distribution of observation for 50% leaf drop, whereas the Japanese and Kuril groups combined to produce a normal distribution with the Kuril group, bridging a gap between clusters of early and late Japanese genotypes. Several Russian genotypes were significantly earlier than all Japanese and Kuril genotypes, but others overlapped with the earliest Japanese genotype (J-444-39). R-27-35 coincided with several Japanese genotypes but was significantly later than all other Russian genotypes and earlier than all Kuril genotypes. No statistical differences were detected between any Kuril genotypes, and there was a broad range for the Japanese group with some statistical differences between the earliest and latest genotypes.

There were some statistical differences at 95% leaf drop within the Russian group. Notably, R-27-35 was later than all others. There was no overlap between Russian and Japanese groups, but there were statistical differences between the earliest and latest Japanese genotypes, while the Kuril group was statistically intermediate.

In the Fraser Valley, growth cessation and fruit colouring coincide in the early Russian, intermediate Japanese and late Kuril foundation groups, with the same relative order for the leaf drop phenophase some months later. In Russia, after bud break, a period of rapid shoot elongation is observed at the same time as bloom, growth slowing and undergoing episodic starts and stops before ceasing at approximately the same time as the fruit colouring phenophase (Plekhanova 2000). Similarly, in the Fraser Valley, this episodic growth is observed toward the end of spring shoot growth, but overall quiescence of most shoots on a plant coincides with the fruit colouring phenophase. Early growth cessation, entrance into dormancy and leaf drop are related to low productivity in Russian germplasm compared to the higher yielding Japanese and Kuril groups (**Section 5.2.1.1**) that grow for longer and do not enter dormancy as early.

Due to their adaptation to relatively longer summer days, plants adapted to higher latitudes (50-64° N for the Russian group) tend to end seasonal growth and begin floral initiation sooner than those from lower latitudes (43° N and 45° N for the Japanese and Kuril groups, respectively) when brought under a similar intermediate latitude (49° N in the Fraser Valley). The similar average growth cessation and leaf drop responses for the Japanese and Kuril groups likely reflect their similar southern latitudes of provenances. The much earlier Russian phenology is adaptive to higher latitudes with longer summer day-length (DL) and a shorter growing season.

Low year-to-year variance (unpublished data) suggests a strong role of DL cues in the physiological control of growth cessation and leaf drop, but other factors are likely involved. Particularly, location-to-location variance (unpublished data) suggests an interaction between DL and other region-specific environmental factors that require further study to fully understand. Greenhouse experiments demonstrate that blue honeysuckle can, as for many long-lived perennial tree species with northern adaptation, be artificially induced to cease growth in response to short DL (eight h) to prepare for winter dormancy (unpublished data). Additionally, continuous vegetative growth can be maintained under long DL (18 h) in a greenhouse for many months (unpublished data).

Literature accounts of growth cessation are limited to reports on *kamtschatica* germplasm in the northern environments of Pavlovsk and the Komi Republic. In the former, it occurs at the end of June (19 h DL) (Plekhanova 1989); in the latter, it occurs at the end of June to the beginning of July (20.5-21 h. DL) (Ryabinina 2009). Under field conditions in the Fraser Valley, growth cessation occurs early enough that days are still lengthening, the Russian germplasm reaching growth cessation 28 before the summer solstice. Having finished fruiting, a DL of 15:40 h would be sufficiently short to provide the cue required to initiate dormancy-related processes, but further study is required to understand the control of this trait and the other factors involved.

Literature reports on leaf drop indicate mid-September (12:45 h DL) in Pavlovsk (Firsov 2002); the first half of October (11:20-10:00 h DL) in the Komi Republic (Ryabinina 2009); early September to mid-October (13:40-10:30 h DL) in the Kaluga oblast (Esichev 2009); mid to late September (12:30-11:45 h DL) in the Primorye oblast (Stepanov 2009); mid-October (10:15 h DL) in the Tomskaya oblast (Suchkova and Senina 2009); and late September to early October (11:45-11:00 h DL) in the Mari El Republic (Golovunin 2009). In the Fraser Valley, Russian material reaches this phenophase at approximately the same date and DL (10:50 h) as Tomaskaya (*Dfc*) and the Komi Republic (*Dfa*) with cold and hot summers, respectively, which is later than the Mari El Republic (*Dfb*), Primorye oblast (monsoon-influenced warm-summer humid continental climate – *Dwb*), Pavlovsk (*Dfa*) and Kaluga oblast (*Dfb*) with longer DL. As for growth cessation, no simple explanation based on latitudes of Russian germplasm provenance can be used to fully explain the contrasts in leaf drop across a range of continental climates compared to the temperate climate of the Fraser Valley. Nonetheless, interaction of a DL cue with the onset of cool fall temperatures is supported by greenhouse experimental data showing quicker progression to leaf drop in blue

honeysuckle accessions treated with cool temperatures and short DL than short DL alone (unpublished data).

From field observations, once Russian germplasm ceases to grow, the plants quickly begin to deteriorate under the hot, often dry, conditions of the following three months in the Fraser Valley. The leaves of most genotypes became scorched and turned black, especially at the Langley trial site with well-drained soil. These plants enter a state of stress-related eco-dormancy (unpublished data) to survive until conditions once again become conducive to growth. Entering the winter, these plants are weakened by a prolonged period with reduced photosynthetic activity and sporadic, premature breaking of buds during the late summer and early fall months. In addition, early flushes of bud break during the late fall and early winter months, resulting from fulfillment of their minimal chilling requirement (unpublished data), results in winter damage. These factors lead to reduced vigour, limiting annual shoot growth in the following year, which confirms observations in Corvallis, OR (Thompson and Barney 2007). This is adaptationally problematic because incremental annual growth is a primary determinant of productivity in the following year (Prischepina 2000). As the tallest Eurasian taxon, *kamtschatica* bush height is observed to reach 2.0 m in colder climates (Pojarkova 1958). Based on field observations of the current trials in the Fraser Valley in 2017, Russian plants have seldom reached 1.0 m, even after seven years in the field. For Russian germplasm with early phenology, damage accumulates because of adaptation to higher latitudes and shorter growing seasons, leading to vegetative atrophy and episodes of premature bud break from eco-dormancy in late summer/early fall and from endo-dormancy in late fall/early winter. This results in low vigour in the next growing season and poor yields in subsequent years. Later phenologies in the Japanese and Kuril groups evolved in regions with longer growing seasons and shorter summer days. Consequently, when brought to the intermediate latitude of the Fraser Valley, they are not as severely affected by temperate climatic conditions as the Russian germplasm.

4.2.2.2 Blueberry, Raspberry and Strawberry Compared to Foundation Germplasm

The absolute phenotypic range in growth cessation was spread over ten days for the Russian group, six days for the Japanese group and less than two days for the Kuril group (**Figure 4.2**; **Table 4.5**). Correspondingly, 50% and 95% leaf drop were spread over long periods of four and two weeks for the Russian group; moderate twenty and six day periods for the Japanese group;

70

and short three and one day periods for the Kuril group. In comparison, the blueberry cultivars were spread over 21 and 11 days. 'Duke' reached 50% leaf drop at the same time as several of the later Japanese genotypes. However, the other three cultivars were significantly later than all blue honeysuckle (**Appendix B.8**). All four blueberry cultivars reached 95% leaf drop significantly later than all blue honeysuckle. The raspberry cultivars reached 50% and 95% leaf drop over 11 and 16 day spans, respectively, and were significantly later than any blue honeysuckle.

Related to early growth cessation, blue honeysuckle begins floral initiation at a very early date in contrast with blueberry, raspberry and strawberry for which floral bud development is triggered by a combination of cool temperatures and shorter DL usually observed in late summer and early fall. In blue honeysuckle, growth cessation is followed by a very rapid (35-45 days in Pavlovsk) sequence of flower bud set and differentiation that more readily leads to secondary summer flowering if environmental conditions (i.e., water, nutrients and light) prompt release from eco-dormancy and new flushes of vegetative growth (Plekhanova 1989). In the Fraser Valley, this sporadic growth is observed in the field to produce secondary flowering as early as mid-July, but later flushes in August and September are more likely to generate flowers that produce ripe fruit in early fall. This fruit is typically low in quantity and quality, making it negligible as a second crop. As observed in Pavlovsk (Plekhanova 1989), these new shoots usually harden off by the time winter arrives, but whether the degree of subsequent floral initiation for the following year varies across germplasm groups is not known. Release from eco-dormancy is observed in all three foundation groups, but this phenomenon must be differentiated from the Russian group's tendency to release from endo-dormancy in the late fall/early winter due to a low chill requirement. The latter occurs after endo-dormancy peaks and directly limits total yield in the following year (Plekhanova 2000).

The original provenance of all three foundation groups were cold climates with shorter growing seasons than the Fraser Valley, which has an intermediate latitude (49° N) to the more southern Japanese and Kuril groups (43° and 45° N, respectively) and more northern Russian group (50-64° N). Since floral initiation occurs before the summer solstice, independence of floral bud set from a critical DL or temperature cue is suggested. Therefore, blue honeysuckle's rapid initiation of floral structures directly following growth cessation is likely related to its adaptation to cold continental climates with short growing seasons for germplasm adapted to higher latitudes with longer summer DL as well as to lower latitudes with shorter summer DL.

71

4.2.2.3 Out-group Comparisons to Foundation Germplasm:

J-PP reached growth cessation at the same as the three earliest Japanese genotypes but later than all Russian genotypes except R-27-35 (**Appendix B.8**). All three U of S cultivars were in the same range as the later Japanese and earlier Kuril genotypes. 'Borealis' was later than J-PP and all Russian genotypes. 'Tundra' was later than J-PP and all Russian genotypes except R-27-35. 'Indigo Gem' was earlier than 'Borealis' but not different from J-PP or R-27-35.

J-PP reached 50% and 95% leaf drop intermediate to the earliest and latest Russian genotypes though significantly earlier than R-27-35 and all Japanese and Kuril genotypes. 'Borealis' reached 50% leaf drop at the same time as R-27-35 and one other Russian genotype, but was as late as only two Japanese and none of the Kuril genotypes. Though not statistically different from 'Borealis', the other two U of S cultivars were later than J-PP, earlier than R-27-35 and the same as only the earliest in the Japanese group. At 95% leaf drop, all three U of S cultivars were later than J-PP and all but R-27-35 and one other Russian genotype while significantly earlier than all Japanese and Kuril genotypes.

As for the spring phenophases, J-PP and the U of S cultivars show intermediate timing for growth cessation and leaf drop between the early Russian and late Japanese and Kuril groups. J-PP's phenology demonstrates the existence of sources of earlier phenology within Japanese germplasm, which shows a high degree of temperate climate adaptation. The U of S cultivars demonstrate the ability to introgress useful traits from the maladapted Russian material by hybridization with later Kuril germplasm, but does not further demonstrate the underlying genetic control of these traits.

4.2.3   Spring Phenology of Improved Germplasm
4.2.3.1 Parent Genotype Contrasts for Improved Germplasm Families

For the eight Japanese/Kuril families, the Kuril parent was significantly later than the Japanese parent for each estimate of bud break, but at flowering onset and fruit colouring/harvest only six were significantly later, with one earlier and the other statistically equivalent, except at 90% flowering onset when both were significantly earlier (**Appendix B.9**). Across all three spring phenophases, the Japanese parent was significantly later than the Russian parent for all 16 Japanese/Russian families, and the Kuril parent was significantly later than the Russian parent for all 16 Kuril/Russian families. Therefore, for each spring phenophase, almost all improved families

were combinations of statistically different parent genotypes as expected from their membership in the early Russian, intermediate Japanese and late Kuril foundation groups.

4.2.3.2 Absolute Range, Group Extremes and Heritability

For the three estimates of bud break, the absolute earliest improved genotypes were in the Kuril/Russian group followed closely by the Japanese/Russian group and the Japanese/Kuril group. The absolute latest were in the Japanese/Russian group, preceded by four to six days by the Japanese/Kuril group and the Kuril/Russian group (**Figure 4.3**; **Table 4.6**). For flowering onset, the absolute earliest genotype was in the Kuril/Russian group followed a week later by the Japanese/Kuril and Japanese/Russian groups. The absolute latest were in the Japanese/Kuril group, but the late extremes in the other two groups were not far behind (**Table 4.7**). For fruit colouring/harvest, the absolute earliest were in the Kuril/Russian group followed a week or more later by the other two groups. The absolute latest were in the Japanese/Kuril and Japanese/Russian groups with the latest in the Kuril/Russian group a week to ten days earlier (**Table 4.8**). For the foundation and improved germplasm overall, the earliest and latest extremes for bud break and first open flower were in the Russian and Kuril groups, respectively. In contrast, 30% and 90% flowering onset and each estimate of fruit colouring/harvest had broader overall germplasm ranges (27-33 days) than either the foundation (27-32 days) or improved (25-31 days) germplasm on their own because the earliest and latest were in the Kuril/Russian and Kuril groups, respectively.

For each estimate of the three spring phenophases, H^2 was high to very high for all foundation and improved groups combined and in each foundation group on its own, but it ranged from moderate to very high in each improved group on its own (**Table 4.9**). In individual germplasm groups, H^2 varied from negligible to high, depending on the combination of phenophase and group. For the improved groups combined, h^2 was moderate for all three estimates of bud break and low for each estimate of flowering onset and fruit colouring/harvest, whereas it was negligible for each improved group for bud break and fruit colouring/harvest and moderate to high in Japanese/Kuril group on its own.

Complexity of adaption to a temperate climate was demonstrated in the improved groups by variation in the absolute range of observations within and across phenophases and compared with their parental foundation groups. There was a more compact absolute range of observations in the Japanese/Kuril and Kuril/Russian groups than the Japanese/Russian group at bud break, but
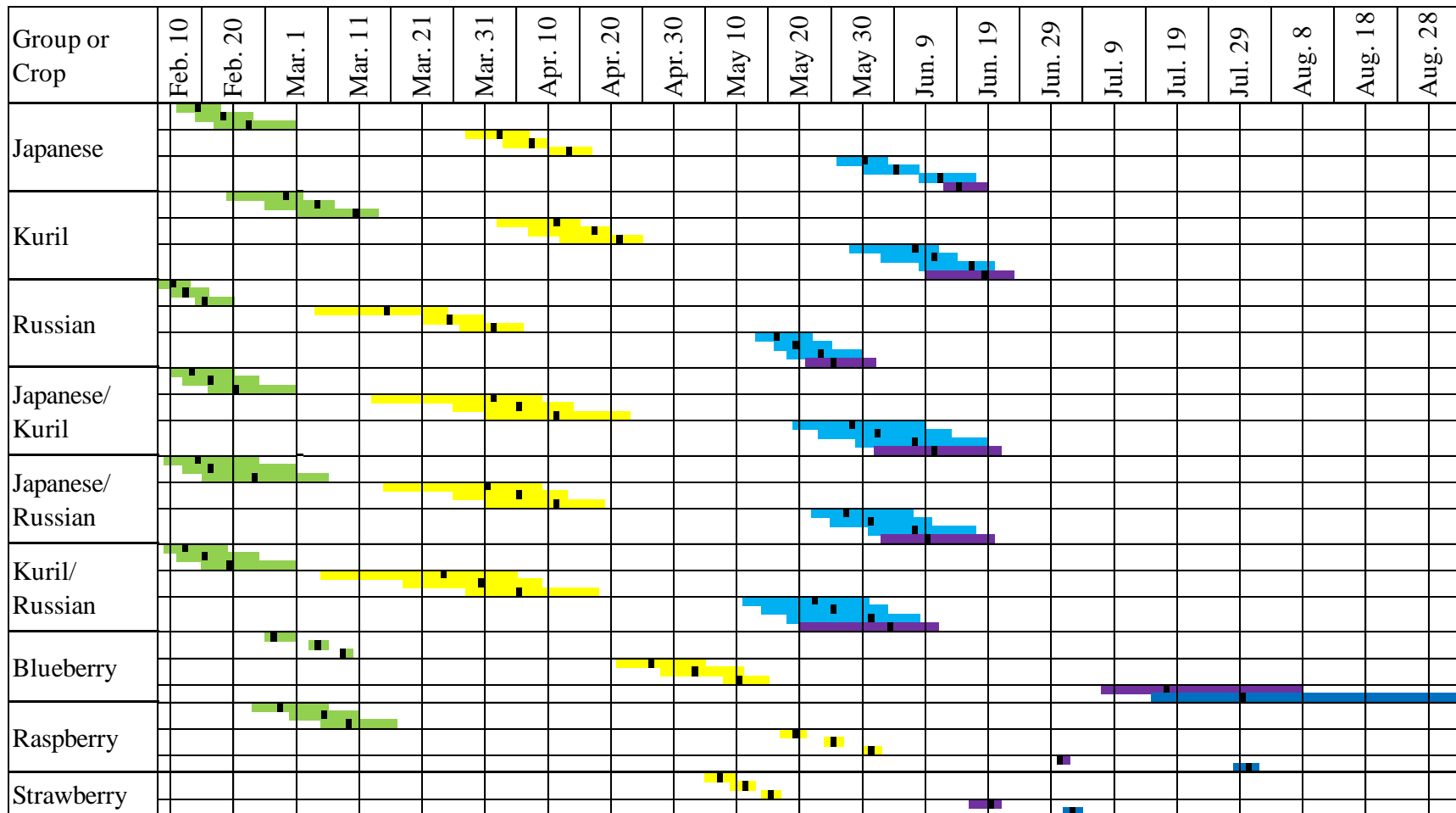
Figure 4.3. Foundation and Improved Germplasm: Spring phenology in blue honeysuckle and comparison crops in 2012/2013 in the Chilliwack, BC, Canada (bars represent the range of genotypes for each group or crop with the group average indicated by a black bar, ▮ – bud break (top – 10%, centre – 50%, bottom – 90%), ▮ – flowering onset (top – first open flower, centre – 30%, bottom – 90%), ▮ – fruit colouring (top – 50%, centre – 75%, bottom – 100%), ▮ – simultaneous blue honeysuckle and first comparison crop harvest, ▮ – final comparison crop harvest).

74

Table 4.6. Foundation and Improved Germplasm: Bud break phenophase in blue honeysuckle groups and comparison crops in 2012/2013 in Chilliwack, BC, Canada.

Group	Japanese	Kuril	Russian	Japanese/ Kuril	Japanese/ Russian	Kuril/ Russian	Blueberry	Raspberry
10% Bud Break								
Average	Feb. 14	Feb. 27	Feb. 10	Feb. 13	Feb. 15	Feb. 12	Feb. 26	Feb. 27
Median	Feb. 14	Mar. 1	Feb. 10	Feb. 12	Feb. 15	Feb. 12	Feb. 26	Feb. 27
Minimum	Feb. 11	Feb. 19	Feb. 8	Feb. 10	Feb. 9	Feb. 9	Feb. 25	Feb. 23
Maximum	Feb. 17	Mar. 1	Feb. 12	Feb. 19	Feb. 23	Feb. 18	Feb. 28	Mar. 4
Range (days)	6.1	10.5	3.8	9.1	14.1	8.8	3.2	9.3
50% Bud Break								
Average	Feb. 18	Mar. 4	Feb. 12	Feb. 16	Feb. 17	Feb. 15	Mar. 4	Mar. 5
Median	Feb. 18	Mar. 5	Feb. 12	Feb. 15	Feb. 18	Feb. 15	Mar. 4	Mar. 4
Minimum	Feb. 14	Feb. 25	Feb. 10	Feb. 12	Feb. 12	Feb. 11	Mar. 3	Feb. 28
Maximum	Feb. 22	Mar. 6	Feb. 15	Feb. 23	Feb. 28	Feb. 23	Mar. 5	Mar. 10
Range (days)	7.7	9.3	4.9	10.8	15.8	11.6	2.4	10.1
90% Bud Break								
Average	Feb. 22	Mar. 10	Feb. 15	Feb. 20	Feb. 23	Feb. 19	Mar. 8	Mar. 9
Median	Feb. 22	Mar. 12	Feb. 15	Feb. 19	Feb. 23	Feb. 18	Mar. 8	Mar. 8
Minimum	Feb. 17	Mar. 1	Feb. 14	Feb. 16	Feb. 15	Feb. 15	Mar. 8	Mar. 5
Maximum	Feb. 28	Mar. 13	Feb. 19	Feb. 28	Mar. 4	Feb. 28	Mar. 9	Mar. 16
Range (days)	9.7	12.3	5.6	11.8	16.9	13.0	1.9	10.4

Table 4.7. Foundation and Improved Germplasm: Flowering onset phenophase in blue honeysuckle groups and comparison crops in 2012/2013 in Chilliwack, BC, Canada.

Group	Japanese	Kuril	Russian	Japanese/ Kuril	Japanese/ Russian	Kuril/ Russian	Blue-berry	Rasp-berry	Straw-berry
First Open Flower									
Average	Apr. 2	Apr. 11	Mar. 15	Apr. 1	Mar. 31	Mar. 24	Apr. 26	May. 19	May. 7
Median	Apr. 3	Apr. 13	Mar. 16	Apr. 3	Mar. 31	Mar. 25	Apr. 25	May. 19	May. 6
Minimum	Mar. 27	Apr. 2	Mar. 4	Mar. 13	Mar. 15	Mar. 5	Apr. 21	May. 17	May. 5
Maximum	Apr. 6	Apr. 14	Mar. 24	Apr. 8	Apr. 8	Apr. 4	May. 5	May. 20	May. 9
Range (days)	10.4	11.6	18.8	25.1	24.0	30.3	13.8	3.1	3
30% Flowering Onset									
Average	Apr. 7	Apr. 17	Mar. 25	Apr. 5	Apr. 5	Mar. 30	May. 3	May. 25	May. 11
Median	Apr. 6	Apr. 19	Mar. 25	Apr. 6	Apr. 4	Mar. 30	May. 3	May. 26	May. 11
Minimum	Apr. 3	Apr. 7	Mar. 21	Mar. 26	Mar. 26	Mar. 18	Apr. 28	May. 24	May. 9
Maximum	Apr. 9	Apr. 19	Mar. 30	Apr. 13	Apr. 12	Apr. 8	May. 10	May. 26	May. 12
Range (days)	6.3	12.2	9.4	17.2	16.5	20.2	12.1	2.4	3
90% Flowering Onset									
Average	Apr. 13	Apr. 21	Apr. 1	Apr. 11	Apr. 11	Apr. 5	May. 10	May. 31	May. 15
Median	Apr. 14	Apr. 24	Apr. 2	Apr. 12	Apr. 11	Apr. 4	May. 9	May. 31	May. 15
Minimum	Apr. 10	Apr. 12	Mar. 28	Mar. 31	Mar. 31	Mar. 28	May. 8	May. 30	May. 14
Maximum	Apr. 16	Apr. 24	Apr. 5	Apr. 22	Apr. 18	Apr. 17	May. 14	Jun. 1	May. 16
Range (days)	5.7	12.9	7.9	22.1	17.7	19.9	6.6	2.0	2

Table 4.8. Foundation and Improved Germplasm: Fruit colouring/harvest phenophases in blue honeysuckle groups and comparison crops in 2012/2013 in Chilliwack, BC, Canada.

Group	Japanese	Kuril	Russian	Japanese/ Kuril	Japanese/ Russian	Kuril/ Russian
50% Blue Fruit						
Average	May. 30	Jun. 7	May. 16	May. 28	May. 27	May. 22
Median	May. 30	Jun. 9	May. 16	May. 28	May. 27	May. 22
Minimum	May. 26	May. 28	May. 13	May. 19	May. 22	May. 11
Maximum	Jun. 2	Jun. 10	May. 21	Jun. 8	Jun. 6	May. 30
Range (days)	6.8	13.0	8.1	20.6	14.9	18.4
75% Blue Fruit						
Average	Jun. 4	Jun. 10	May. 19	Jun. 1	May. 31	May. 25
Median	Jun. 4	Jun. 12	May. 19	Jun. 1	May. 30	May. 26
Minimum	May. 30	Jun. 2	May. 16	May. 23	May. 25	May. 14
Maximum	Jun. 7	Jun. 13	May. 24	Jun. 12	Jun. 9	Jun. 2
Range (days)	7.4	11.0	8.0	19.9	15.1	18.8
100% Blue Fruit						
Average	Jun. 11	Jun. 16	May. 23	Jun. 7	Jun. 7	May. 31
Median	Jun. 11	Jun. 18	May. 23	Jun. 9	Jun. 5	Jun. 1
Minimum	Jun. 8	Jun. 7	May. 18	May. 29	May. 31	May. 18
Maximum	Jun. 16	Jun. 19	May. 29	Jun. 18	Jun. 16	Jun. 7
Range (days)	7.2	12.0	9.6	20.1	16.3	20.5

Table 4.8. Continued. Foundation and Improved Germplasm: Fruit colouring/harvest phenophases in blue honeysuckle groups and comparison crops in 2012/2013 in Chilliwack, BC, Canada.

Group	Japanese	Kuril	Russian	Japanese/ Kuril	Japanese/ Russian	Kuril/ Russian
Sole Harvest for Blue Honeysuckle						
Average	Jun. 14	Jun. 18	May. 25	Jun. 10	Jun. 9	Jun. 3
Median	Jun. 14	Jun. 20	May. 25	Jun. 12	Jun. 8	Jun. 4
Minimum	Jun. 12	Jun. 9	May. 21	Jun. 1	Jun. 2	May. 20
Maximum	Jun. 18	Jun. 22	May. 31	Jun. 20	Jun. 19	Jun. 10
Range (days)	6.3	13.0	9.7	19.0	16.3	21.0

Group	Blue-berry	Rasp-berry	Straw-berry
First Harvest for Comparison Crops			
Average	Jul. 17	Jun. 30	Jun. 19
Median	Jul. 11	Jun. 30	Jun. 19
Minimum	Jul. 7	Jul. 30	Jun. 16
Maximum	Aug. 7	Jul. 1	Jun. 20
Range (days)	31.1	0.5	4.2
Final Harvest for Comparison Crops			
Average	Jul. 29	Jul. 30	Jul. 2
Median	Jul. 20	Jul. 29	Jul. 1
Minimum	Jul. 15	Jul. 28	Jul. 1
Maximum	Sept. 1	Jul. 31	Jul. 3
Range (days)	48.1	2.8	2.0

Table 4.9. Foundation and Improved Germplasm: Heritability estimates for spring phenophases across blue honeysuckle groups alone and in combination in 2012/2013 in Chilliwack, BC, Canada (H^2 – broad-sense heritability calculated from linear mixed model regression, h^2 – narrow-sense heritability calculated from mid-parent regression of phenotypic averages[1]).

	10% Bud Break		50% Bud Break		90% Bud Break		First Open Flower		30% Flowering Onset		90% Flowering Onset		50% Blue Fruit		75% Blue Fruit		100% Blue Fruit		Fruit Harvest	
	H^2	h^2	H^2	h^2	H^2	h^2	H^2	h^2	H^2	h^2	H^2	h^2	H^2	h^2	H^2	h^2	H^2	h^2	H^2	h^2
All Germplasm	0.94	-	0.87	-	0.88	-	0.88	-	0.73	-	0.92	-	0.73	-	0.74	-	0.90	-	0.90	-
All Foundation	0.91	-	0.90	-	0.95	-	0.92	-	0.86	-	0.97	-	0.84	-	0.82	-	0.92	-	0.91	-
Japanese	0.83	-	0.70	-	0.80	-	0.45	-	0.22	-	0.76	-	0.40	-	0.43	-	0.36	-	0.29	-
Kuril	0.18	-	0.18	-	0.46	-	0.73	-	0.83	-	0.97	-	0.72	-	0.58	-	0.91	-	0.87	-
Russian	0.17	-	0.52	-	0.85	-	0.73	-	0.30	-	0.43	-	0.05	-	0.03	-	0.09	-	0.09	-
All Improved	0.93	0.53	0.83	0.49	0.82	0.50	0.86	0.27	0.68	0.38	0.90	0.38	0.68	0.27	0.71	0.29	0.88	0.32	0.89	0.32
Japanese/Kuril	0.94	0.00	0.90	0.00	0.89	0.00	0.38	0.56	0.23	0.62	0.82	0.47	0.71	0.00	0.65	0.00	0.68	0.00	0.64	0.00
Japanese/Russian	0.89	0.14	0.89	0.16	0.86	0.19	0.88	0.00	0.74	0.01	0.90	0.00	0.65	0.04	0.67	0.03	0.86	0.00	0.86	0.02
Kuril/Russian	0.77	0.11	0.66	0.09	0.66	0.05	0.88	0.00	0.65	0.09	0.86	0.10	0.56	0.00	0.64	0.00	0.88	0.00	0.91	0.00

[1]Different regression models were used to calculate H^2 and h^2 heritability estimates, so these measures are not directly comparable.

this shifted over the course of the flowering onset phenophase, resulting in a shorter absolute range in the Japanese/Russian group than the other improved groups for the fruit colouring/harvest phenophase. For bud break, the absolute ranges for the Kuril, Japanese and Russian groups were narrow, moderate and broad, respectively, and the ranges for each improved group were about as broad as for the Kuril group. For flowering onset and fruit colouring/harvest, the absolute ranges for each improved group was broader than for the foundation groups. These shifts emphasized the need to understand the complexity of adaptive responses to a temperate climate and interpret the utility of each foundation group based on how they combine to produce unique improved group phenotypes on a phenophase by phenophase basis.

Moreover, although H^2 was consistently high to very high for each phenophase when all foundation and improved groups were combined and for each foundation group on its own, it varied from moderate to very high, depending on the specific combination of improved group and phenophase. For bud break, H^2 was highest for the Japanese, Russian and Japanese/Kuril groups, moderate for the Japanese/Russian and Kuril/Russian groups and low for the Kuril group. For flowering onset, the Kuril and Japanese/Russian groups had the highest H^2, while it was moderate to high for the Kuril/Russian group and ranged from negligible to high for the Japanese, Russian and Japanese/Kuril groups. For fruit colouring/harvest, the Kuril group consistently had the highest H^2, while it was low and negligible for the Japanese and Russian groups, respectively. For fruit colouring, H^2 was moderate to high for all three improved groups and for harvest it was very high, high and moderate for the Kuril/Russian, Japanese/Russian and Japanese/Kuril groups, respectively. Therefore, selecting for spring phenology phenotypes should be met with relative success for any of the three improved groups. The Japanese/Kuril group showed higher H^2 than the other groups for bud break, more variable H^2 for flowering onset and lower H^2 for fruit harvest. The Kuril/Russian group was noted for its very high H^2 for date of harvest. On a longer time-frame, across improved groups there was moderate h^2 for bud break and low h^2 for flowering onset and fruit colouring/harvest, suggesting potential difficulty in making additive genetic gains through selection within improved groups. On the other hand, the Japanese/Kuril group showed moderate to high h^2 on its own for flowering onset, suggesting the potential to make additive gains in bloom period through selection.

4.2.3.2 Improved Japanese/Kuril Germplasm

The Japanese/Kuril group reached each determination of bud break over a range of 9-12 days, flowering onset over 17-25 days and fruit colouring/harvest over 19-21 days (**Table 4.6**; **Table 4.7**; **Table 4.8**). The earliest Japanese/Kuril genotype reached bud break one to two days before the earliest Japanese genotype, and the latest was on the same day or a day before even the earliest Kuril genotype but one to two days after the latest Japanese genotype. For flowering onset, the earliest Japanese/Kuril genotype reached each estimate seven to thirteen days before the earliest Japanese genotype, while the latest was two to seven days before the latest Kuril genotype. At fruit colouring/harvest, the earliest Japanese/Kuril genotype was seven to eleven days before the earliest Japanese genotype, and the latest was one to two days before the latest Kuril genotype.

There were no late transgressive segregants for any estimate of bud break, but the proportions of the common early-parent types and rare late-parent types decreased over the course of the phenophase as the proportion of intermediates and early transgressive segregants increased (**Figure 4.4**; **Appendix B.10**). Similarly, at flowering onset, there was a considerable number of early transgressive segregants and early-parent types, no late transgressive segregants and few to no late-parent types, which left half or more as intermediates. Finally, at fruit colouring/harvest, there were considerably more early than late transgressive segregants and far more early than late-parent types, leaving a quarter to a third as intermediates.

Across spring phenology, comparison of each Japanese/Kuril genotype to its actual parents demonstrated a heavy skew toward dominance and overdominance of intermediate Japanese over late Kuril phenology. The earliest Japanese/Kuril genotypes coincided with the earliest Japanese genotypes, but the latest did not quite overlap with even the earliest Kuril genotype at bud break, only overlapped the earliest Kuril genotype at flowering onset and almost overlapped the latest Kuril genotype at fruit colouring/harvest.

Across bud break, early transgressive segregants were increasingly distinctive from their Japanese parents, but there was a decrease in distinctiveness between the early and late-parent types and their respective Japanese and Kuril parents. Equally, across flowering onset, the early Japanese/Kuril genotypes were increasingly distinct from their early Japanese and late Kuril parent groups. As fruit colouring/harvest progressed, there was a further broadening of the distinctions between the earliest Japanese/Kuril genotypes and the late Kuril group and a narrowing of difference between the latest Japanese/Kuril genotypes and the earlier Japanese group with an

81
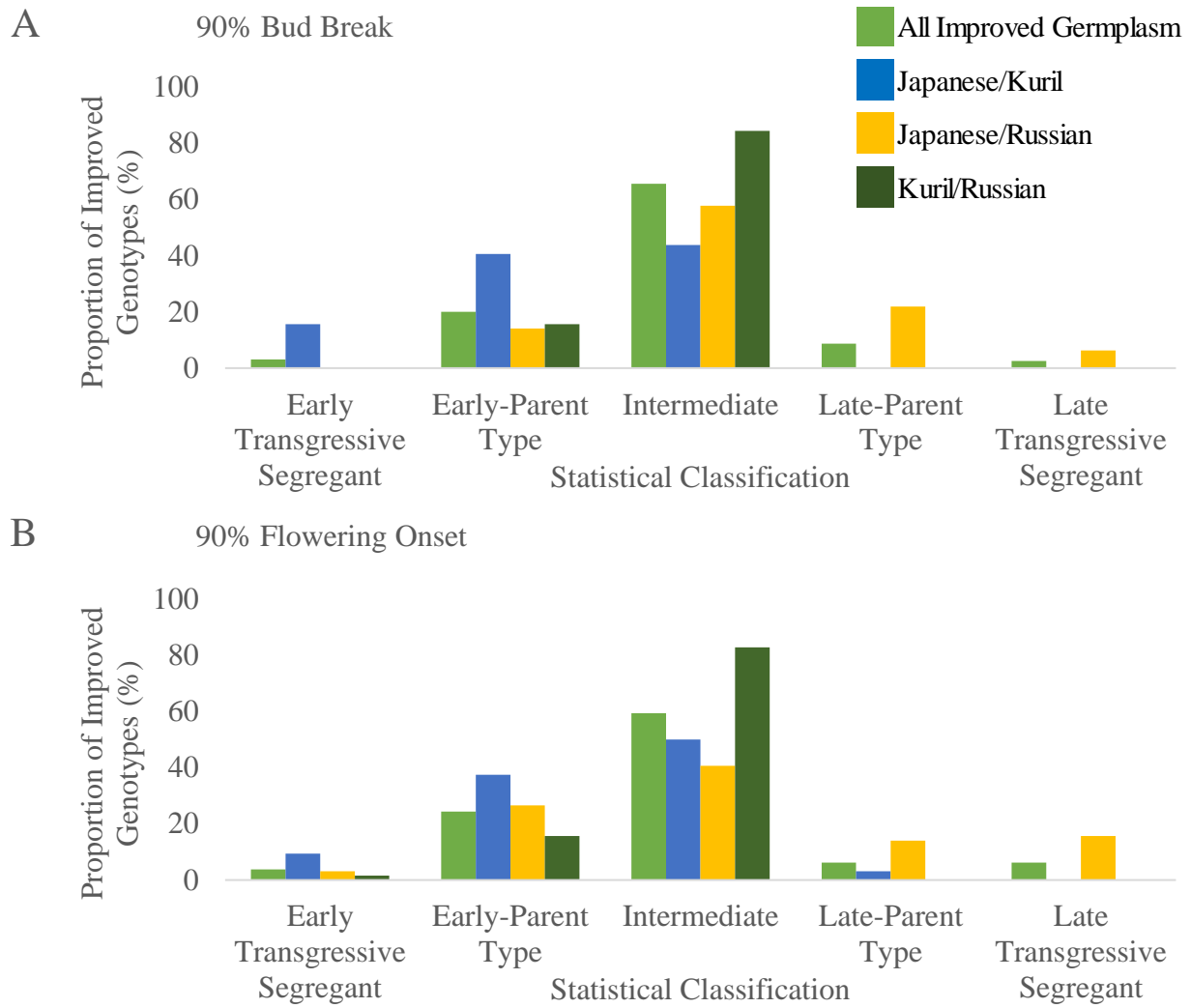
Figure 4.4. Improved Germplasm: Statistical classification of blue honeysuckle hybrids compared to their parent genotypes for spring phenology in 2012/2013 in Chilliwack, BC, Canada. (A) 90% bud break (B) 90% flowering onset (C) 50% Fruit colouring (D) Fruit harvest.
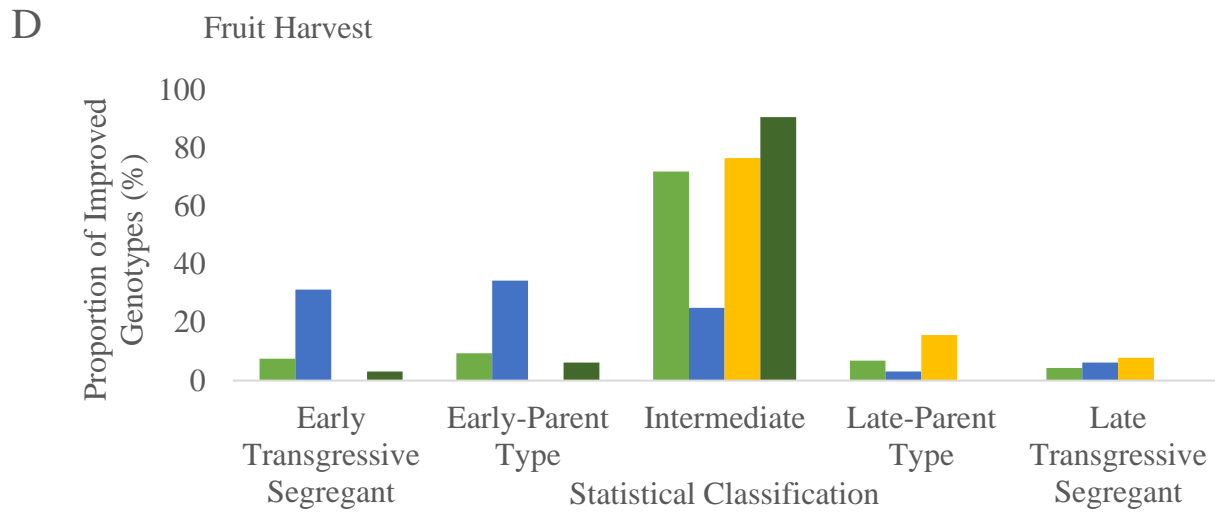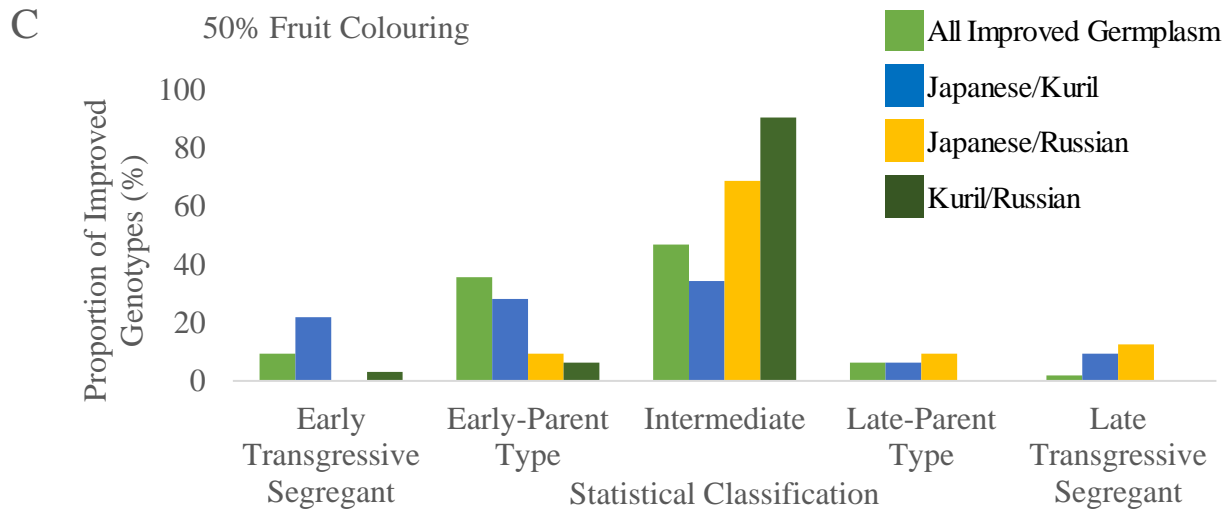
Figure 4.4. Continued. Improved Germplasm: Statistical classification of blue honeysuckle hybrids compared to their parent genotypes for spring phenology in 2012/2013 in Chilliwack, BC, Canada. (A) 90% bud break (B) 90% flowering onset (C) 50% Fruit colouring (D) Fruit harvest.

increase in both early-parent types and transgressive segregants.

Comparing across phenophases, for bud break and flowering onset, there was a skew toward early transgressive segregants and parent types with no late transgressive segregants and few late-parent types, with almost a third and more than half as intermediates, respectively. For fruit colouring/harvest, there was an even stronger skew toward early transgressive segregants, though some late transgressive segregants were observed, and there was still a predominance of early-parent types over late, with less than a third remaining as intermediates. While the skew toward early-parent types was greater at bud break than at flowering onset and fruit colouring/harvest, the proportion of early transgressive segregants was greater at fruit colouring/harvest than at flowering onset or bud break. Conversely, despite increasing slightly over the phenophases, there were little to no late-parent types with late transgressive segregants only observed at fruit colouring/harvest. The proportion of intermediates was approximately a third at both bud break and fruit colouring/harvest and half or more at flowering onset. Therefore, skew in the Japanese/Kuril group toward earlier Japanese phenology at bud break was less pronounced at flowering onset and fruit colouring/harvest, but there was a broader range in extreme phenologies, especially early transgressive segregation, for the latter phenophase.

4.2.3.3 Improved Japanese/Russian Germplasm

The Japanese/Russian group reached each successive estimate of bud break over a range of 14-17 days (**Table 4.6)**, flowering onset over 17-24 days (**Table 4.7)** and fruit colouring/harvest over 15-16 days (**Table 4.8**). The earliest Japanese/Russian genotype reached bud break a day after the earliest Russian genotype, while the latest was five to seven days later than the latest Japanese genotype. The earliest Japanese/Russian genotype reached flowering onset three to eleven days after the earliest Russian genotype and the latest was two to three days later than the latest Japanese genotype, as at bud break. At fruit colouring/harvest, the earliest Japanese/Russian genotype was nine to twelve days after the earliest Russian genotype and the latest was zero to four days later than the latest Japanese genotype.

At bud break, there were some late and no early transgressive segregants, more late- than early-parent types and mostly intermediates (**Figure 4.4**; **Appendix B.10**). Late transgressive segregation increased over the flowering onset phenophase as the proportion of late-parent types decreased. Early transgressive segregants were negligible and the proportions of early-parent

types and intermediates fluctuated. At fruit colouring/harvest, there were no early transgressive segregants at all, but there were some late transgressive segregants. The number of early-parent types decreased and late-parent types increased over the course of the phenophase, intermediates ranging from two thirds to three quarters. Overall, for each spring phenophase, there was skew toward late transgressive segregants and late-parent types with little to no early transgressive segregants and few early-parent types, whereas half to three quarters were intermediates.

The Japanese/Russian group showed skew toward intermediate Japanese over early Russian phenology, a mirror image of the Japanese/Kuril group, but demonstrated a fluctuating degree of dominance and overdominance of later phenology across the spring phenophases. For each estimate of each phenophase, the earliest Japanese/Russian genotypes coincided with only the later Russian genotypes, though the latest Japanese/Russian genotypes completely overlapped the phenology of the intermediate Japanese group.

Across bud break, aside from fluctuations in the number of intermediates that affected the proportions of early and late-parent types, the proportion of late transgressive segregants remained constant and there were no early transgressive segregants. By first open flower, there was a skew toward late-parent types over early-parent types with neither early nor late transgressive segregants, but there were equal proportions of earlier and later types by 90% flowering onset. Across fruit colouring/harvest, there was a substantial skew toward late transgressive segregants, but there were the same proportions of early- and late-parent types at 50% blue fruit, whereas there were no early-parent types by 100% blue fruit and harvest.

Across phenophases, the distinctions between the Japanese and Russian groups were narrower at bud break than flowering onset. Therefore, the slight tendency in the Japanese/Russian group toward later Japanese phenology showed up as both dominance and overdominance at bud break with a greater role of the latter manifesting at flowering onset. In contrast, along with some skew toward overdominance of later phenology, there was much more additive gene action for fruit colouring/harvest. However, no skew toward dominance of later phenology was detected at 50% blue but a considerable degree was observed at the end of the phenophase.

The skew toward later Japanese phenology shifted considerably for the Japanese/Russian group over the course of the spring phenophases but not in a single direction. At bud break, there was some dominance and overdominance of later Japanese phenology over the earlier Russian phenology, but primarily overdominance of late phenology was seen at flowering onset. For fruit

85

colouring/harvest, there was a less pronounced skew toward overdominance of later phenology and the skew toward dominance of later phenology only manifested at the end of the phenophase.

4.2.3.4 Improved Kuril/Russian Germplasm

The Kuril/Russian group reached bud break over a range of nine to thirteen days (**Table 4.6)**, flowering onset over 20-30 days (**Table 4.7)** and fruit colouring/harvest over 18-21 days (**Table 4.8**). The earliest Kuril/Russian genotype reached bud break a day after the earliest Russian genotype, whereas the latest was one to two days earlier than the earliest Kuril genotype. The earliest Kuril/Russian genotype reached flowering onset a day after to three days before the earliest Russian genotype and the latest was seven to eleven days earlier than the latest Kuril. The earliest Kuril/Russian genotype reached fruit colouring/harvest one to two days before the earliest Russian genotype and the latest was 11-12 days earlier than the latest Kuril genotype.

There were no early or late transgressive segregants or late-parent types for any estimate of bud break as the majority were either intermediates or early-parent types (**Figure 4.4**; **Appendix B.10**). Similarly, at flowering onset, there were negligible proportions of early transgressive segregants and no late transgressive segregants, while there was a moderate number of early-parent types far outnumbering the occasional late-parent type, but intermediates still predominated. Further, there was a clear majority of intermediates at fruit colouring/harvest, with less skew toward early-parent types but a slightly greater proportion of early transgressive segregants than at bud break or flowering onset, and there were neither late-parent types nor late transgressive segregants. Overall, for bud break and flowering onset, there was skew toward early-parent types with few to no early transgressive segregants, no late transgressive segregants or late-parent types and a large majority intermediates. In comparison, fruit colouring/harvest showed a less pronounced skew toward early-parent types, approximately the same skew toward early transgressive segregants and a similar majority of intermediates but neither late transgressive segregants nor late-parent types.

The Kuril/Russian group demonstrated an overwhelmingly intermediate response compared to its parent group extremes in spring phenology. There was only a slight skew toward dominance and overdominance of early Russian phenology, the latter only manifesting at flowering onset and fruit colouring/harvest. Therefore, for all three estimates of bud break, the earliest Kuril/Russian genotype was almost as early as the earliest Russian genotype, while the

latest was earlier than even the earliest Kuril genotype, meaning that there was only overlap with the later Russian and earlier Kuril group. For all but first open flower, when the earliest Kuril/Russian genotype was a day later than the earliest Russian genotype, the early extreme completely overlapped the Russian group but the late extreme did not overlap the latest Kuril genotypes.

Across bud break, there were neither late-parent types nor early nor late transgressive segregants, but the number of early-parent types decreased over the phenophase resulting in a commensurate increase in the proportion of intermediates. For flowering onset, there was also a predominance of intermediates and the proportion of early-parent types remained as at the end of the bud break phenophase. The proportion of intermediates was constant across estimates of fruit colouring/harvest with low numbers of early-parent types and even some early transgressive segregants.

Across phenophases, there was a trend toward a greater additive gene action and a decrease in the substantial skew toward dominance of early phenology initially observed at bud break. The slight skew toward overdominance of early phenology seen during fruit colouring/harvest was negligible compared to this overall pattern. In summary, the Kuril/Russian group produced primarily additive gene action between the late Kuril and early Russian foundation groups with some slight skew toward dominance of early Russian phenology – this skew was greatest at bud break and decreased over the following phenophases.

4.2.3.5 Mode of Gene Action across Improved Germplasm Groups

Intermediate types made up more than half to nearly two thirds of all improved genotypes at bud break and flowering onset, the proportion ranging from under half at 50% blue fruit to almost three quarters through to harvest (**Figure 4.4**; **Appendix B.10**). The proportion of intermediates was highest and most consistent in the Kuril/Russian group, generally increasing over the season. The Japanese/Russian group had a more moderate proportion of intermediates, consistent for bud break and flowering onset and somewhat higher for fruit colouring/harvest. The Japanese/Kuril group had a less consistent proportion of intermediates, being low at 10% and 50% bud break, higher at 90% bud break and flowering onset but much lower for fruit colouring/harvest.

The total incidence of early-parent types was higher than late-parent types for all three phenophases. The proportion of early-parent types was similar across bud break, flowering onset

87

and 50% blue fruit, but considerably lower progressing toward harvest. At bud break, the more abundant early-parent types were primarily in the Japanese/Kuril group. Late-parent types were less abundant and were primarily in the Japanese/Russian group, though some were in the Japanese/Kuril group. At flowering onset, the early-parent types were mostly in the Japanese/Kuril group, but considerable proportions were also seen for the other improved groups. Most late-parent types were in the Japanese/Russian group. There were far more early-parent types at 50% blue fruit than at other determinations of the phenophase, and most were in the Japanese/Russian group with smaller proportions in the other improved groups. For the rest of the fruit colouring/harvest phenophase, early-parent types were mostly in the Japanese/Kuril and some in the Japanese/Russian group. Across fruit colouring/harvest, most of the late-parent types were in the Japanese/Russian group and a small number in the Japanese/Kuril group.

The total incidence of transgressive segregation was low across the three estimates of bud break, increased over the course of the flowering onset phenophase and remained higher across fruit colouring/harvest. For all three spring phenophases, most transgressive segregation was due to early transgressive segregants in the Japanese/Kuril group and late transgressive segregants in the Japanese/Russian group.

Across the spring phenophases, the foundation groups combined in various ways to produce different phenotypes in the improved groups. There was a strong tendency toward dominance of earlier Japanese genetics over later Kuril genetics in the Japanese/Kuril group. There was less pronounced dominance of later Japanese genetics over earlier Russian genetics in the Japanese/Russian group and, contrastingly, of earlier Russian genetics over later Kuril genetics in the Kuril/Russian group.

Across all improved groups, the proportion of intermediates increased slightly over the spring phenophases, but this was primarily because of increases in the Kuril/Russian and Japanese/Russian groups. Early-parent types were most pervasive in the Japanese/Kuril group, followed by the Japanese/Russian group, and little to none in the Kuril/Russian group, depending on the phenophase. Late-parent types were most prevalent in the Japanese/Russian group for all phenophases, with much fewer in the Japanese/Kuril group and almost none in the Kuril/Russian group. Transgressive segregation was largely due to combination of either the early Russian group or late Kuril group with the intermediate Japanese group, resulting in overdominance for lateness and earliness, respectively. This shows a tendency for the intermediate Japanese genetics to

moderate the extreme phenology of the early and late groups by producing transgressive segregants toward the opposite extreme. In contrast, the early and late foundation groups combined predominantly additive gene action.

For the combination of intermediate and late foundation groups, the Japanese/Kuril group demonstrated strong dominance and some overdominance of intermediate Japanese phenology over late Kuril phenology. Equally, for the combination of intermediate and early foundation groups, the Japanese/Russian group presented a genetic mirror image, but with slight differences across the phenophases. At bud break, there was dominance and overdominance of intermediate phenology over early but to a lesser degree than was seen over the late phenology in the Japanese/Kuril group. At flowering onset, there was still slight dominance of intermediate phenology but no overdominance. At fruit colouring/harvest, there were primarily additive gene action with some dominance and overdominance of relatively later phenology. Compared to the other groups, the Kuril/Russian group showed more additive gene action between early and late phenology that increased as the season progressed. There was some dominance of early Russian phenology over late Kuril phenology that decreased across phenophases. A low degree of overdominance of early phenology was seen for the later phenophases. Overall, the intermediate Japanese phenology was dominant and overdominant when combined with both early Russian and late Kuril phenologies, but these latter two groups combined to make intermediate phenotypes with skew toward dominance of early Russian phenology at bud break that was quite negligible by fruit colouring/harvest.

4.2.3.6 Blueberry, Raspberry and Strawberry Compared to Improved Germplasm

The blueberry cultivars reached the three determinations of bud break two to three days before the latest in the improved groups, only the latest Kuril genotypes in the foundation germplasm demonstrating some overlap (**Figure 4.3**; **Table 4.6**). They reached flowering onset starting eight to fourteen days after the latest Kuril genotype and 13-20 days after the latest in the improved groups (**Table 4.7**). The earliest initial and final harvests were 15 and 33 days after the latest Kuril genotype and 17 and 35 days after the latest improved genotype, respectively (**Table 4.8**).

The earliest raspberry cultivar coincided with the latest improved genotype (a Japanese/Russian) at only 10% bud break, while overlapping the Kuril group average by a day or

two for all three estimates. In contrast, the raspberry cultivars reached flowering onset 33-36 days after the latest Kuril genotype and 38-41 days after the latest improved genotype. The earliest initial raspberry harvest was eight and ten days after the latest Kuril and Japanese/Kuril genotypes, respectively, final raspberry harvest occurring 36 and 38 days later than the last blue honeysuckle.

The three successive estimates of flowering onset in the strawberry cultivars started 20-21 and 22-27 days after the latest Kuril and Japanese/Kuril genotypes, respectively. Compared to the latest Kuril and Japanese/Kuril harvests, the earliest initial strawberry harvest was six and four days earlier, respectively, and earliest final strawberry harvests was nine and eleven days later. Compared to the earliest Russian and Kuril/Russian genotypes, the earliest initial harvest was 26 and 27 days later, respectively, and earliest final harvest was 41 and 42 days later.

Therefore, at bud break, there was no overlap between any of the improved groups and the blueberry cultivars, but the latest Japanese/Russian genotype reached 10% and 50% bud break as late as the earliest raspberry cultivar. No improved group overlapped with the three comparison crops for the flowering onset phenophase, but the Japanese/Kuril and Japanese/Russian groups overlapped with the strawberry cultivars for initial harvest, final harvest in this crop stretching much later than any of the blue honeysuckle germplasm.

4.2.4   Vegetative Growth Cessation and Leaf Drop of Improved Germplasm
4.2.4.1 Parent Genotype Contrasts for Improved Germplasm Families

For growth cessation, the Japanese parent was significantly later than the Kuril for a single Japanese/Kuril family, whereas the parents were statistically equivalent for seven other families (**Appendix B.9**). At 50% and 95% leaf drop, there were four and five Japanese/Kuril families with a significantly earlier Japanese parent; one and three with no statistical differences; and two and one with a significantly later Japanese parent. Therefore, though the parent combinations used in making the Japanese/Kuril group did not contrast distinctly at growth cessation, the majority had an earlier Japanese parent at leaf drop. In contrast, for both growth cessation and leaf drop, the Russian parent was significantly earlier than the Japanese and Kuril parents for all Russian/Japanese and Kuril/Russian families, respectively.

4.2.4.2 Absolute Range, Group Extremes and Heritability

For growth cessation, 50% and 95% leaf drop, the absolute earliest improved genotype was in the Kuril/Russian group, followed closely by the other improved groups (**Figure 4.5**; **Table 4.10**). The latest growth cessation was on the same date in each improved group, but the Japanese/Kuril group had the latest leaf drop.

H^2 was high for growth cessation and very high for leaf drop for the foundation and improved germplasm combined and the foundation germplasm on its own, but it was moderate for growth cessation and very high for leaf drop for the improved germplasm on its own (**Table 4.11**). For growth cessation, H^2 was low, negligible and moderate for the Japanese, Kuril and Russian groups, respectively, and low, moderate and high for the Japanese/Kuril, Japanese/Russian and Kuril/Russian groups, respectively. In contrast, for leaf drop, H^2 was high, moderate to high and very high for the Japanese, Kuril and Russian groups, respectively, and high for the Japanese/Kuril group and very high for the other improved groups.

The similar absolute ranges and phenotypic averages for growth cessation and leaf drop in each improved group demonstrate relatively simpler control of these phenological traits compared to spring phenology, supporting the findings of the foundation germplasm trials (**Section 4.2.2**). For growth cessation in specific, though differences in population size between the foundation and improved germplasm sizes restrict direct comparison, all three improved groups had broader ranges in growth cessation than the foundation groups, pointing to dissortive recombination for a trait that is stabilized in the foundation groups. On the premise that DL has an important role in controlling growth cessation, adaptation to a restricted range of latitudes is likely under strong stabilizing natural selection in the wild. Similar phenotypic averages were observed across the three improved groups, which suggests additive variation in the foundation groups. When the foundation groups are combined, their stabilized responses to environmental cues recombined to result in a broad array of phenotypes that centre around a similar average, mid-way between the earlier Russian group and the later Japanese and Kuril groups. This supports the concept that these foundation groups represent different eco-geographic subspecies of the same species (Plekhanova 1994a) that diverged through adaptive radiation as they moved out from the centre of origin in the Russian Far East (Sabitov 1986). The genetic diversity for growth cessation, tendency toward a moderate average phenotypic response and considerable H^2 in improved groups suggest selection for this trait should be met with relative success. Directional selection toward later growth

Group or Crop	May 20	May 30	Jun. 9	Jun. 19	Jun. 29	Jul. 9	Jul. 19	Jul. 29	Aug. 8	Aug. 18	Aug. 28	Sept. 7	Sept. 17	Sept. 27	Oct. 7	Oct. 17	Oct. 27	Nov. 6	Nov. 16	Nov. 26
Japanese																				
Kuril																				
Russian																				
Japanese/ Kuril																				
Japanese/ Russian																				
Kuril/ Russian																				
Blueberry																				
Raspberry																				
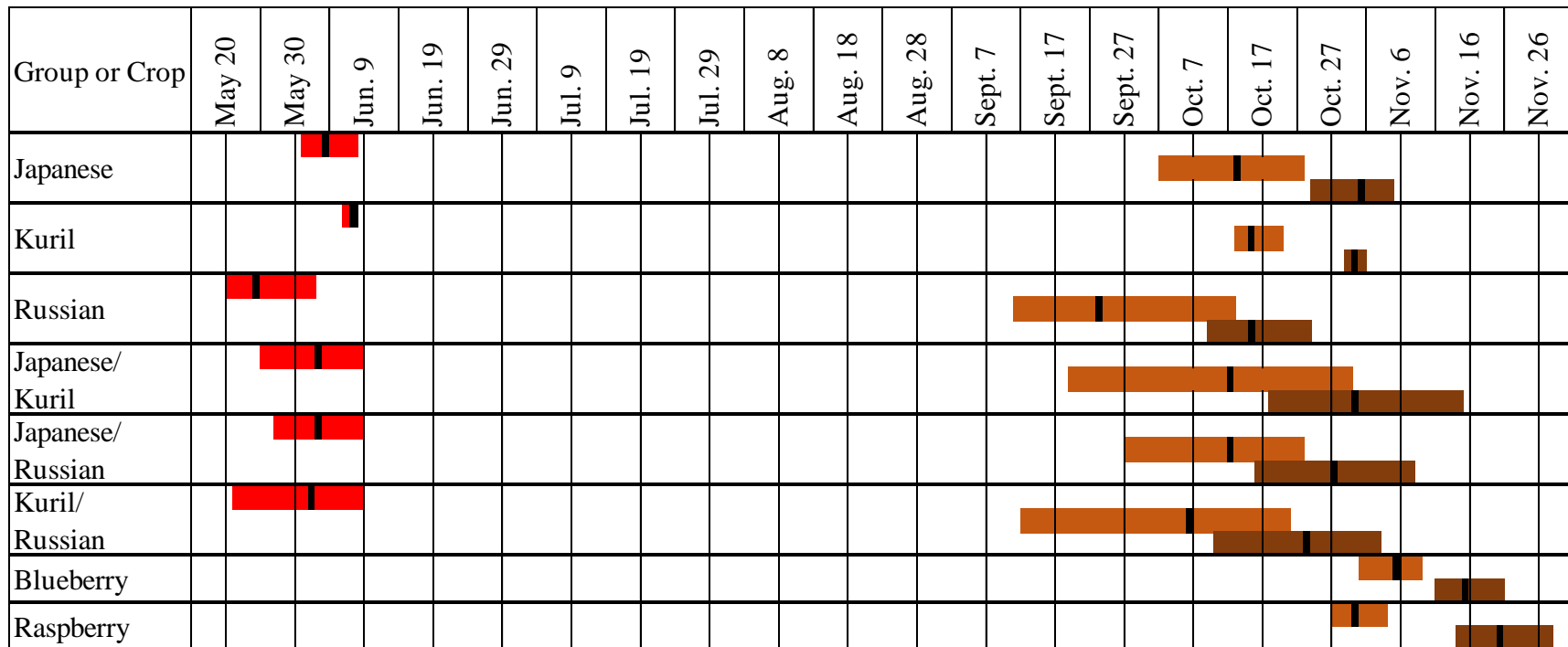
Figure 4.5. Foundation and Improved Germplasm: Growth cessation and leaf drop in blue honeysuckle and comparison crops in 2012/2013 in the Chilliwack, BC, Canada (bars represent the range of phenotypic averages for each group with the group average indicated by a black bar. ▮ – vegetative growth cessation (end of major flush of early season growth), ▮ – 50% leaf drop, ▮ – 95% leaf drop).

Table 4.10. Foundation and Improved Germplasm: Vegetative growth cessation and leaf drop phenophases in blue honeysuckle and comparison crops in 2012/2013 in Chilliwack, BC, Canada.

Group	Japanese	Kuril	Russian	Japanese/ Kuril	Japanese/ Russian	Kuril/ Russian	Blue-berry	Rasp-berry
Growth Cessation								
Average	May. 4	Jun. 7	May. 24	Jun. 2	Jun. 2	Jun. 1	-	-
Median	May. 6	Jun. 7	May. 23	Jun. 3	Jun. 2	Jun. 2	-	-
Minimum	May. 31	Jun. 6	May. 20	May. 25	May. 27	May. 21	-	-
Maximum	Jun. 7	Jun. 7	Jun. 1	Jun. 8	Jun. 8	Jun. 8	-	-
Range (days)	7.2	1.3	11.4	14.3	12.6	18.7	-	-
50% Leaf Drop								
Average	Oct. 13	Oct. 15	Sept. 23	Oct. 12	Oct. 12	Oct. 6	Nov. 5	Oct. 30
Median	Oct. 12	Oct. 15	Sept. 23	Oct. 14	Oct. 12	Oct. 7	Nov. 5	Oct. 30
Minimum	Oct. 2	Oct. 13	Sept. 11	Sept. 19	Sept. 27	Sept. 12	Oct. 31	Oct. 27
Maximum	Oct. 22	Oct. 19	Oct. 12	Oct. 29	Oct. 22	Oct. 20	Nov. 8	Nov. 3
Range (days)	20.1	6.2	31.3	39.8	25.0	37.4	7.9	7.1
95% Leaf Drop								
Average	Oct. 31	Oct. 30	Oct. 15	Oct. 30	Oct. 27	Oct. 23	Nov. 15	Nov. 20
Median	Nov. 1	Oct. 30	Oct. 16	Oct. 29	Oct. 27	Oct. 23	Nov. 15	Nov. 20
Minimum	Oct. 24	Oct. 29	Oct. 9	Oct. 18	Oct. 16	Oct. 10	Nov. 11	Nov. 14
Maximum	Nov. 4	Oct. 31	Oct. 23	Nov. 14	Nov. 7	Nov. 2	Nov. 20	Nov. 27
Range (days)	10.9	2.3	13.8	26.3	20.9	22.8	9.1	12.4

Table 4.11. Foundation and Improved Germplasm: Broad-sense heritability estimates for growth cessation and leaf drop across blue honeysuckle groups alone and in combination in 2012/2013 in Chilliwack, BC, Canada.

	Growth Cessation	Leaf Drop 50%	Leaf Drop 95%
All Germplasm	0.72	0.95	0.96
All Foundation	0.84	0.97	0.97
Japanese	0.31	0.87	0.71
Kuril	0.01	0.83	0.59
Russian	0.68	0.93	0.93
All Improved	0.68	0.94	0.96
Japanese/Kuril	0.38	0.84	0.84
Japanese/Russian	0.50	0.91	0.96
Kuril/Russian	0.85	0.96	0.93

cessation should also be possible to maintain adaptation to southern latitudes against the average tendency seen in these improved groups. This should not be difficult given the higher H^2 observed in the two improved groups with a Russian parent, which contributes the most northern latitudinal adaptation.

4.2.4.3 Improved Japanese/Kuril Germplasm

The Japanese/Kuril group reached growth cessation over 14 days (**Table 4.10**). The dates for 50% and 95% leaf drop ranged 40 and 26 days, respectively. For growth cessation, the earliest Japanese/Kuril genotype was six and twelve days before the earliest Japanese and Kuril genotypes, respectively, and the latest was a day later than the latest Japanese and Kuril genotypes. The earliest 50% and 95% leaf drop in the Japanese/Kuril group were thirteen and six days before the earliest Japanese genotype and twenty-three and ten days before the earliest Kuril genotype. The latest were seven and ten days after the latest Japanese genotype and ten and thirteen days after the latest Kuril genotype.

For growth cessation, there were no late-parent types or late transgressive segregants at all, whereas there was a high proportion of early transgressive segregants and early-parent types, leaving only a third as intermediates (**Figure 4.6**; **Appendix B.11**). For leaf drop, there were more late transgressive segregants and late-parent types than early, 50% and 95% leaf drop having two fifths and one fifth intermediates, respectively. Total transgressive segregation in growth cessation comprised more than half of genotypes and was entirely seen in early transgressive segregants. At 50% and 95% leaf drop, total transgressive segregation was about a fifth and a third, respectively, being made up of a third early transgressive segregants and two thirds late transgressive segregants in both cases.

For growth cessation, the assortive combination of Japanese and Kuril foundation groups resulted in an extreme expression of overdominance of early growth cessation and a lower degree of accompanying dominance. Consequently, the Japanese/Kuril group completely overlapped the range of both parental foundation groups. Contrasting with growth cessation, dominance and overdominance of late phenology was observed for both measures of leaf drop with more pronounced dominance at 50% than 95%. The improved group's very broad range overlapped the extremes of both groups.

95
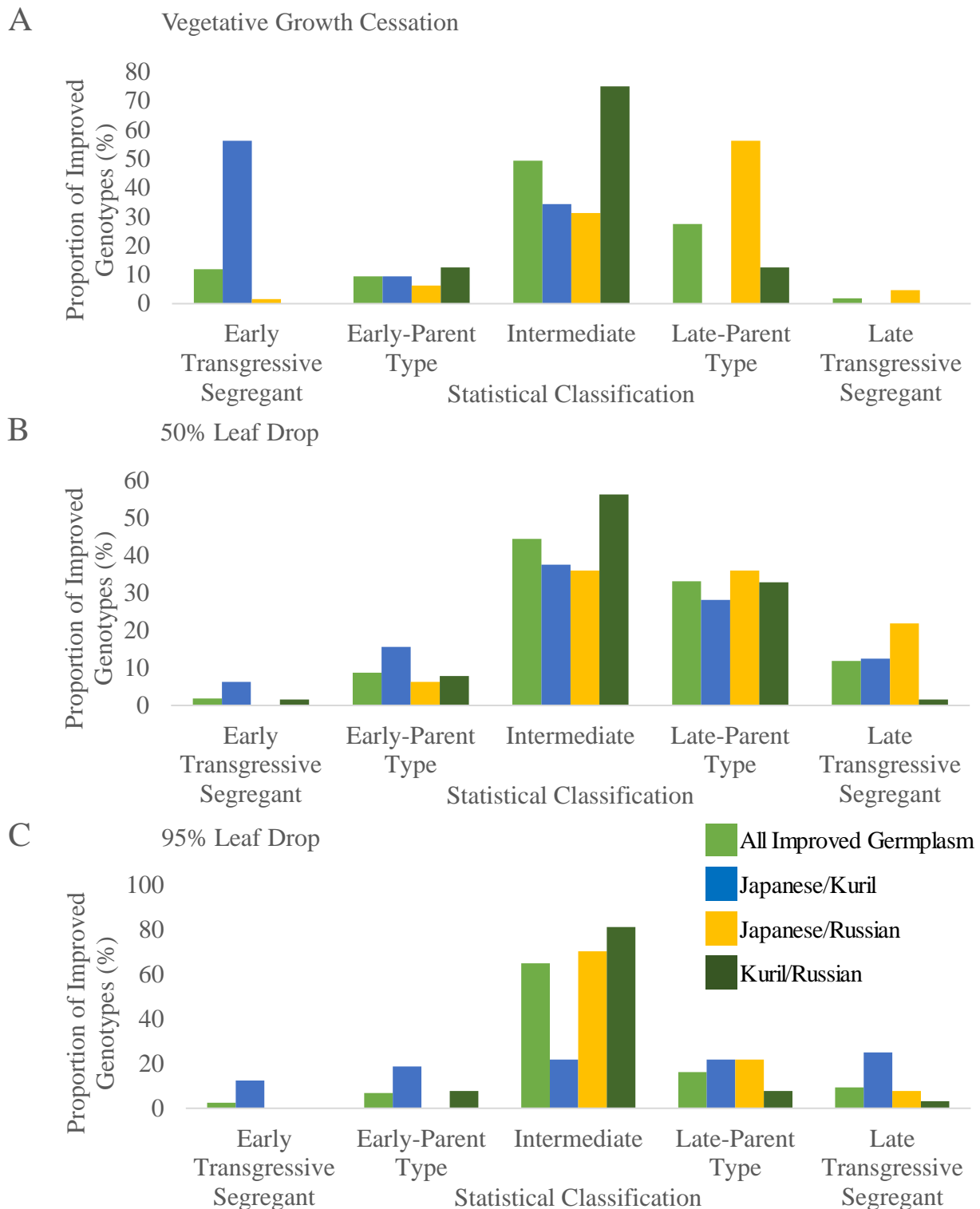
Figure 4.6. Improved Germplasm: Statistical classification of blue honeysuckle hybrids compared to parent genotypes for late-season phenology in 2012/2013 in Chilliwack, BC, Canada. (A) Growth cessation (B) 50% leaf drop (C) 95% leaf drop.

4.2.4.4 Improved Japanese/Russian Germplasm

The Japanese/Russian group reached growth cessation over 13 days (**Table 4.10**). Dates for 50% and 95% leaf drop ranged 25 and 21 days, respectively. For growth cessation, the earliest Japanese/Russian genotype was four days earlier and four days later than the earliest Japanese and Russian genotypes, respectively, and the latest was one and seven days later than the latest Japanese and Russian genotypes. The earliest 50% and 95% leaf drop were five and seven days earlier than the earliest Japanese genotype and sixteen and eight days later than the earliest Russian genotype. The latest was on the same day and two days later than the latest Japanese genotype for 50% and 95% leaf drop, respectively, and ten and fifteen days later than the latest Russian genotype.

For growth cessation, there were only a few early and late transgressive segregants with a massive skew toward late-parent types and less than a third intermediates (**Figure 4.6**; **Appendix B.11**). For leaf drop, there were quite a few late transgressive segregants and no early transgressive segregants, and there were more late- than early-parent types with more than one third and two thirds intermediates for 50% and 95% leaf drop, respectively. Total transgressive segregation at growth cessation and 95% leaf drop was low, while it was nearly a quarter at 50% leaf drop, which was due almost exclusively to late transgressive segregants.

The dissortive combination of Japanese and Russian foundation groups showed a very high degree of dominance of later Japanese growth cessation. This resulted in a phenotypic range that was similar in magnitude to that of the diverse Russian group but that did not overlap the early extreme of the Russian group. Dominance and overdominance of later phenology was seen at 50% leaf drop, but these were much reduced at 95% leaf drop, which was predominated by additive gene action. At 50% leaf drop, the range in Japanese/Russian genotypes was intermediate in magnitude between the two foundation groups, not overlapping the earliest Russian genotype but equalling the Japanese group's latest extreme. The range in 95% leaf drop was broader than either foundation group, coinciding with the latest Japanese but not the earliest Russian genotype.

4.2.4.5 Improved Kuril/Russian Germplasm

The Kuril/Russian group reached growth cessation over 19 days (**Table 4.10**). Dates for 50% and 95% leaf drop ranged 37 and 23 days, respectively. The earliest Kuril/Russian genotype reached growth cessation on the same date as the earliest Russian genotype and sixteen days earlier

than the earliest Kuril genotype, and the latest was one and seven days later than the latest Kuril and Russian genotypes, respectively. The earliest 50% and 95% leaf drop were 31 and 19 days earlier than the earliest Kuril genotype and a day before the earliest Russian genotype, while the latest was one and two days later than the latest Kuril genotype and eight and ten days later than the latest Russian genotype.

For growth cessation, there were no transgressive segregants and there were the same proportions of early- and late-parent types, leaving three quarters as intermediates (**Figure 4.6**; **Appendix B.11**). For leaf drop, there were few early or late transgressive segregants with late-parent types outweighing early-parent types at 50% leaf drop but not 95% leaf drop, most being intermediates.

For growth cessation, the dissortive combination of Kuril and Russian foundation groups showed no overdominance and no skew in dominance but predominating additive gene action. Dominance of later Kuril phenology was seen at 50% leaf drop with a considerable proportion of additive gene action, which characterized an overwhelming majority of improved genotypes at 95% leaf drop. For growth cessation and both estimates of leaf drop, the broad range in Kuril/Russian phenology did not quite reach the early extremes of the Russian group but slightly overlapped the later extremes of the Kuril group.

4.2.4.6 Mode of Gene Action across Improved Germplasm Groups

At growth cessation, intermediates comprised half the improved germplasm overall, the Kuril/Russian group having more than twice the proportion of the other improved groups (**Figure 4.6**; **Appendix B.11**). Intermediate types were slightly less than half and more than half at 50% and 95% leaf drop, respectively.

For growth cessation, the proportion of early- and late-parent types were a tenth and a quarter, respectively, the former spreading across the three improved groups and the latter residing mostly in the Japanese/Russian group. For leaf drop, early-parent types were about three times less common than late-parent types overall, though both types were found in all three improved groups. Early-parent types were most prevalent in the Japanese/Kuril group, and late-parent types were about as pervasive across groups for 50% leaf drop and more common in the Japanese/Kuril group at 95% leaf drop.

Averaged across the improved groups, there was a high proportion of early transgressive segregation at growth cessation and a low proportion at leaf drop, which was due mostly to the Japanese/Kuril group for both phenophases. Late transgressive segregants were very rare and found exclusively in the Japanese/Russian group for growth cessation, but they were discovered in high proportions at leaf drop and in both the Japanese/Russian and Japanese/Kuril groups.

As for the spring phenophases, the foundation groups combined in different ways for the growth cessation and leaf drop phenophases, but not necessarily to produce a different range of improved phenotypes. For growth cessation, overdominance of early phenology in the assortive cross between Japanese and Kuril foundation groups contrasted with dominance of later Japanese phenology when combined with the Russian group, whereas additive gene action was commonly observed between the most phenotypically disparate combination of Russian and Kuril groups. The Japanese/Kuril and Japanese/Russian groups showed similar proportions of additive gene action, half as much as for the Kuril/Russian group. Only the Japanese/Kuril group showed extensive transgressive segregation, inclined toward earlier phenology, and only the Japanese/Russian group showed considerable dominance, disposed toward later phenology. In the assortive combination between the Japanese and Kuril groups, the range of improved genotypes overlapped both groups, but in the dissortive crosses with the Russian group neither the Japanese/Russian nor Kuril/Russian groups overlapped the earliest extremes in the Russian group. Therefore, all foundation group combinations resulted in a very broad range of phenotypic responses that had similar intermediate averages for growth cessation resulting from unique modes of genetic action for each combination of foundation groups.

For leaf drop, dominance and overdominance of late phenology was seen for the assortive cross between the Japanese and Kuril groups and the dissortive cross between the Japanese and Russian groups with greater dominance at 50% and more additive gene action at 95% leaf drop. In contrast, for the dissortive cross between the Russian and Kuril groups, there was dominance of later phenology at 50% but primarily additive gene action at 95% leaf drop. Skew toward dominance of late phenology was seen in all cases, except for the Kuril/Russian group at 95% leaf drop. However, overdominance of late phenology was only substantial for the Japanese/Kuril and Japanese/Russian groups with additive gene action predominating in the Kuril/Russian group as for growth cessation. While the Kuril group is very phenotypically distinct from other blue honeysuckle taxa, these findings have inference for the group's placement within the blue

honeysuckle species complex. The taxonomic status of the Kuril group is unsettled, but these findings support the view that these forms are merely an extreme version of ssp. *kamtschatica* with niche-adaptation to island conditions and southern latitudes, as proposed by Plekhanova (1986b). Overall, the foundation groups combined to produce wide ranges in leaf drop phenology and skew toward dominance and overdominance of later phenology except when the Kuril and Russian groups combined, which resulted in primarily additive gene action that may be related to a closer taxonomic relationship between these groups despite the disparity in their phenologies.

4.2.4.7 Blueberries and Raspberries Compared to Improved Germplasm

No comparisons with other crops were made for growth cessation, but the blueberry and raspberry cultivars were compared for leaf drop (**Figure 4.5**; **Table 4.10**). Estimates of 50% and 95% leaf drop for the blueberry cultivars began nine and seven days after the latest Japanese genotype. Compared to the latest Japanese/Kuril genotype, the earliest blueberry cultivar was two days later for 50% leaf drop and three days earlier for 95% leaf drop. For the raspberry cultivars, 50% and 95% leaf drop began five and eleven days later than the latest Japanese genotype. This was two days earlier than the latest Japanese/Kuril genotype for 50% leaf drop and on the same day for 95% leaf drop. Therefore, for both raspberry and blueberry cultivars, there was no overlap with the blue honeysuckle germplasm at 50% leaf drop, but there was slight overlap with the latest improved genotypes at 95% leaf drop.

Earlier leaf drop than either blueberry or raspberry is not surprising for a northern crop like blue honeysuckle that has cold climate adaption. Earlier entrance into dormancy is not a direct limitation to temperate climate adaptation but is associated with germplasm that does not remain dormant during fluctuating winter temperatures after satisfaction of chilling requirement. Therefore, efforts should be made to select against early growth cessation and leaf drop phenology to breed for better adaptation to temperate climates. The later range in Japanese/Kuril leaf drop phenology that coincided with the blueberry and raspberry cultivars suggests that shifting breeding populations toward later phenology is attainable. Also, the skew in improved germplasm groups toward late leaf drop phenology will facilitate generation of later phenotypes.

100

5. CHAPTER 5: FRUIT MORPHOLOGY AND AGRONOMIC POTENTIAL OF BLUE HONEYSUCKLE GERMPLASM

5.1 Introduction

Blue honeysuckle bears a compound accessory fruit that is formed by synanthy of two simple fruit within an enclosing layer of bract tissue called a cupula (Rehder 1903). With mixed buds undergoing floral development in the previous summer, fruit are borne on one to three nodes at the base of spring vegetative shoots (Kolasin and Pozdynakov 1991). Most fruit weigh between 0.4-2.0 g (Thompson 2006a), but larger fruit were recently bred at the University of Saskatchewan (U of S) (Bors et al 2015). Peak yields range from 2-6 kg per plant and plant productivity directly relates to the amount of vigorous new growth generated in the previous season (Prischepina, 2000). Fruit shapes are highly variable, typically being somewhat elongated (e.g., ovate or oblong) or resembling bells, spindles or torpedoes (Plekhanova 1988). A relatively thin skin and soft flesh result in significant barriers to harvestability, shelf life and marketability as a fresh product (Ochmian et al 2008; Zholobova and Khokhyrakova 2009). Consequently, several morphological features present challenges to development of cultivars with adequate agronomic potential for large-scale commercial production. Important knowledge gaps include understanding genetic diversity in agronomic potential in three foundation germplasm groups, the potential to enhance agronomic potential through development of improved germplasm groups and the physiological and genetic complexity of these traits. To facilitate efficient breeding efforts to improve upon the crop's key limitations, fruit morphological traits relating to agronomic potential were evaluated in a temperate climate in the Fraser Valley, British Columbia, Canada.

5.2 Results and Discussion

5.2.1 Quantitative Measures of Agronomic Potential in Foundation Germplasm

5.2.1.1 Description and Comparison of Foundation Germplasm Groups

Fruit yield ranged immensely from 9.8-596.1 g/plant over the two-year average, whereas fruit weight was less variable at 0.61-2.18 g/fruit (**Figure 5.1**; **Table 5.1**). Fruit length and width ranged from 14.76-26.31 mm and 8.78-14.28 mm, respectively. Ranges in fruit length:width, length:weight and width:weight were 1.38-2.62, 11.54-37.51 mm/g and 6.76-18.23 mm/g, respectively (**Figure 5.2**; **Table 5.1**).

The Japanese group had higher average fruit yield, weight and width than the Kuril group,
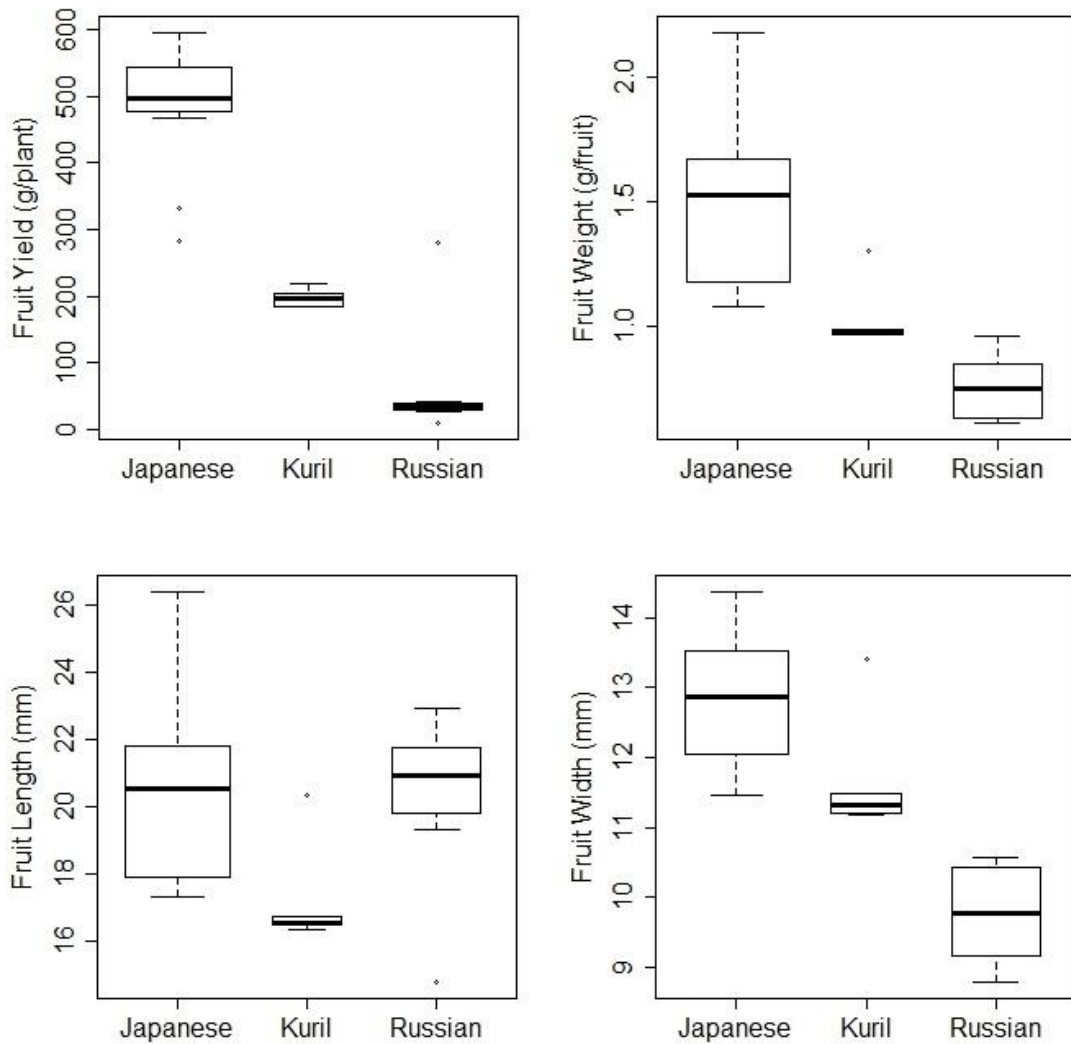
Figure 5.1. Foundation Germplasm: Fruit morphological features in blue honeysuckle evaluated in 2012/2013 in the Fraser Valley, BC, Canada (boxplot widths are proportional to the square root of the sample size for each group).

Table 5.1. Foundation Germplasm: Fruit morphological traits in blue honeysuckle in 2012/2013 in the Fraser Valley, BC, Canada.

Group	Japanese	Kuril	Russian	Group	Japanese	Kuril	Russian
Fruit Yield (g/plant)				Fruit Length:Width			
Average	484.3	198.5	62.5	Average	1.60	1.47	2.08
Median	498.0	197.8	34.4	Median	1.57	1.47	2.12
Minimum	283.4	185.0	9.8	Minimum	1.38	1.44	1.46
Maximum	596.1	219.8	280.0	Maximum	1.87	1.50	2.62
Range	312.7	34.8	270.2	Range	0.49	0.06	1.17
Fruit Weight (g/fruit)				Fruit Length:Weight (mm/g)			
Average	1.52	1.04	0.75	Average	14.08	16.88	28.44
Median	1.52	0.98	0.75	Median	13.86	16.99	27.58
Minimum	1.08	0.97	0.61	Minimum	11.54	15.85	23.10
Maximum	2.18	1.30	0.96	Maximum	16.56	17.42	37.51
Range	1.10	0.34	0.35	Range	5.03	1.57	14.41
Fruit Length (mm)				Fruit Width:Weight (mm/g)			
Average	20.60	17.27	20.33	Average	8.91	11.52	13.85
Median	20.54	16.53	20.92	Median	8.43	11.72	13.65
Minimum	17.29	16.31	14.76	Minimum	6.76	10.58	11.23
Maximum	26.41	20.32	22.92	Maximum	11.11	11.86	18.23
Range	9.12	4.01	8.16	Range	4.35	1.28	7.00
Fruit Width (mm)							
Average	12.85	11.72	9.75				
Median	12.87	11.32	9.76				
Minimum	11.46	11.18	8.78				
Maximum	14.38	13.40	10.57				
Range	2.92	2.22	1.79				
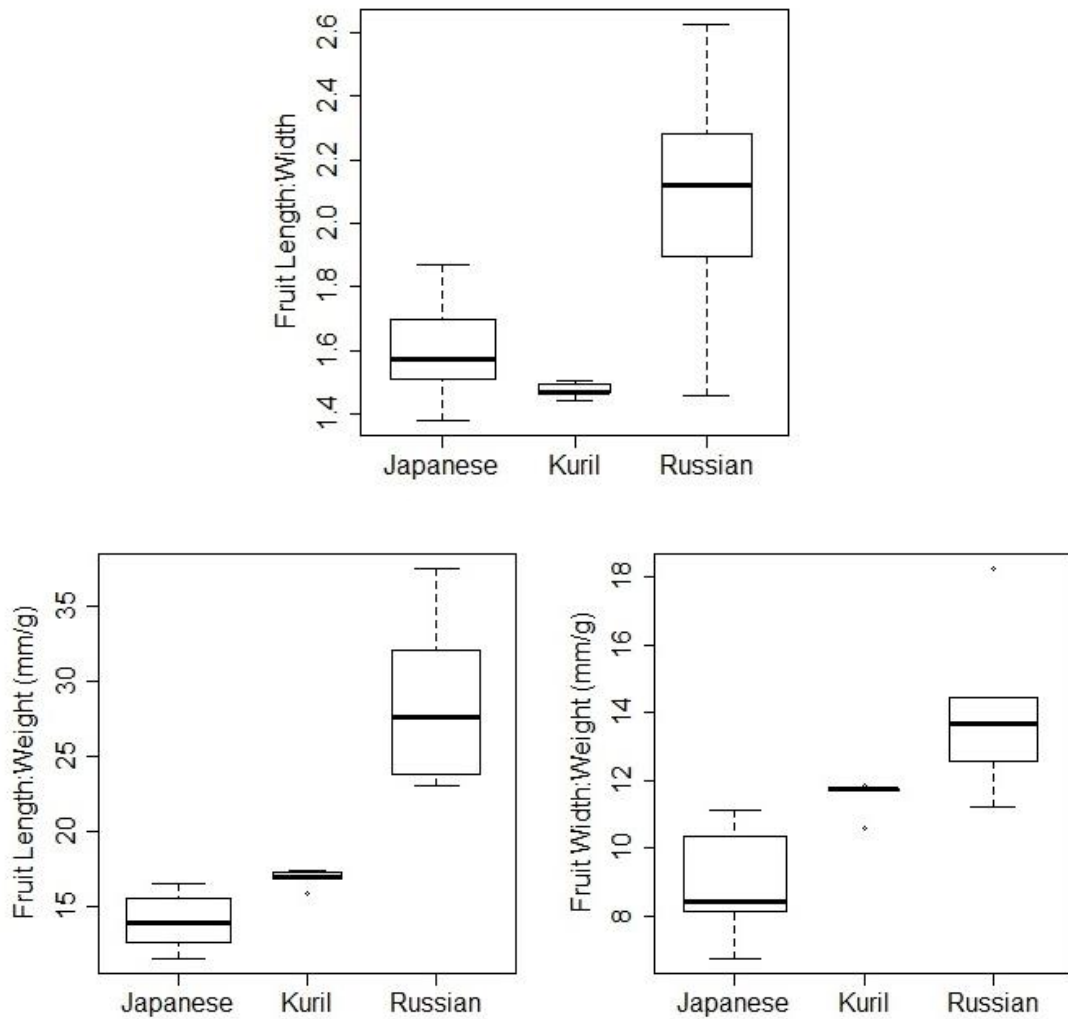
Figure 5.2. Foundation Germplasm: Ratios between fruit morphological features in blue honeysuckle evaluated in 2012/2013 in the Fraser Valley, BC, Canada (boxplot widths are proportional to the square root of the sample size for each group).

and the Russian group had a much lower average for each measure (**Appendix C.1**; **Appendix C.2**). The Japanese and Kuril groups had little variability in yield compared to the Russian group. In contrast, there was a large amount of variation in each group for fruit weight and overlap between multiple genotypes of each group. General distinctions in fruit length could be made between groups despite a high degree of overlap between groups and higher variability for the Japanese and Russian groups than the Kuril group. The Japanese and Russian groups had very similar average lengths, with the longest and shortest fruit being found as Japanese and Russian genotypes, respectively. The average for the Kuril group was shorter than the shortest Japanese genotype and the longest (K-97-12) was close to the average Japanese and Russian genotypes. The range in fruit width was modest for all groups.

Fruit length:width was highest on average for the Russian group and similarly low for the Japanese and Kuril groups (**Appendix C.3**). The range for this ratio was narrowest for the Kuril and broadest for the Russian group, and the Japanese group's range was intermediate in magnitude. The lowest ratios in each group (J-73-39, K-3-05 and R-2-13) were statistically equivalent, but the highest ratio in the Japanese group (J-46-55) was higher than for any of the Kuril genotypes though statistically lower than several high ratios in the Russian group (e.g., R-2-07). Fruit length:weight was higher on average for the Russian than the Kuril group, which was slightly higher than for the Japanese group. As for length:width, the ranges were narrow, moderate, and broad for the Kuril, Japanese and Russian groups, respectively. Approximately half the Japanese genotypes had significantly lower length:weight than the Kuril genotypes, between which there were no statistical differences. As for fruit length:width, the Russian group had a higher average than the Kuril group, and the Japanese group's average was far lower still. In contrast to fruit length:width and length:weight, the Japanese and Russian groups had broader ranges in width:weight relative to their averages, but the Kuril group's range was narrow.

In the Fraser Valley, fruit yield, weight and width were greater in the Japanese than the Kuril group, which were greater than in the Russian group. Fruit length was similar in the Japanese and Russian groups, which were greater than in the Kuril group. These findings contrast with early evaluations at the U of S in a cold continental climate where fruit yield was rated as high for the Russian group, variable for the Japanese group and low for the Kuril group; and fruit weight was rated from medium to small for the Russian group, large to small for the Japanese group and large for the Kuril group (Bors et al 2009).

The Russian fruit were narrower (i.e., greater fruit length:width) than the stout Japanese and Kuril fruit. Correspondingly, the Russian fruit were less dense (i.e., high fruit length:weight and width:weight), meaning the fruit were relatively light for their length and width compared to the dense Japanese fruit. The Kuril fruit were intermediate in density. The stout, dense Japanese fruit also had the greatest weight, length and width. The stout and moderately dense Kuril fruit had modest yields, weights and widths but the lowest lengths. The long, narrow Russian fruit, with low density for their lengths and width, also had the lowest weights and yields. These findings elaborate upon basic observations in the temperate climate in Corvallis, OR (Thompson and Chaovanalikit 2003).

The difference between the Japanese and Russian groups was not just that the former's fruit were stouter but that they were heavier for their length and width. The difference between the Japanese and Kuril groups was not that the former's fruit were stouter but that they were denser, with greater weight per unit length and width. The difference between the Kuril and Russian groups was simply that the fruit of the former were stouter and somewhat denser than those of the latter. Overall, the Japanese group had greater fruit agronomic potential in a temperate climate than the Kuril group, which had more potential than the Russian group. Specifically, the Japanese group's agronomic potential exceeds that of the Kuril group due to greater yield, which are associated with greater length and width, both groups exceeding the Russian group in yield and weight, which are associated with greater width but not length.

5.2.1.2 Japanese Foundation Germplasm

Without clear outliers in yield in the Japanese group, J-41-83 (596.1 g) had the highest and J-56-18 (283.4 g) had the lowest (**Table 5.1**; **Appendix C.1**). This group had the broadest range of fruit weights from 1.08-2.18 g (average 1.52 g). The two heaviest average fruit weights were J-22-14 and J-46-55. There were five Japanese genotypes with intermediate weight (approximately 1.5 g) and four with relatively small fruit (approximately 1.0-1.2 g). Fruit length ranged from 17.3-26.4 mm (average 20.6 mm) (**Appendix C.2**). J-46-55 was significantly longer than J-22-14, and both were significantly longer than the rest of the group, which overlapped with the Russian and Kuril groups. Fruit width ranged from 11.5-14.4 mm (average 12.9 mm). J-22-14 and J-46-55 were statistically wider than all other foundation genotypes. J-41-83, J-42-45, J-

43-87 and J-45-14 were relatively thin. J-21-78, J-444-39, J-56-18, J-66-53 and J-73-39 were intermediate.

Compared with six Japanese genotypes with intermediate fruit length:width, J-46-55, J-66-53 and J-22-14 had significantly higher ratios, and J-73-39 had a significantly lower ratio (**Appendix C.3**). Length:weight was significantly lower for J-22-14, J-444-39, J-46-55, J-56-18 and J-73-39 than J-41-83, J-42-45, J-43-87, J-45-15 and J-66-53 and only J-21-78 was a statistical intermediate. For width:weight, J-22-14 and J-46-55 had the lowest ratios, and J-41-83, J-42-35, J-43-87 and J-45-15 had significantly higher ratios than the rest of the Japanese group.

This broad range in yield observed in the Fraser Valley concurs with observation of variable yields in the Japanese germplasm in Saskatchewan's cold continental climate (Bors et al 2009), and there are similarities in relative yields across these environments as J-41-83 and J-66-53 also had high yields at the U of S (Bors et al 2012). In contrast, greater overall yield potential is suggested for temperate climates since yield in the early years after planting in the Fraser Valley reached the lower end of maximum yield reported in Japan (i.e., 0.5 to 2.0 kg per plant) (Nakajima 1996).

Average fruit weight was lower than a reported maximum size of 3.0 g in Corvallis (Thompson and Chaovanalikit 2003), but there is an important difference between the maximum and average, the latter ranging lower (0.5-2.0 g/fruit) than in the current study (Thompson 2006a). At the U of S, J-66-53, J-73-39 and J-42-45 were rated as medium, medium/small and small, respectively (Bors et al 2012), which shows similar findings across differing climates.

Evaluation of 78 Japanese selections across two locations in Japan showed ranges of fruit weight from 0.37-1.18 g/fruit (average 0.73), length from 11.16-19.43 mm (average 14.65) and width from 7.05-11.74 mm (average 9.42) (Takada et al 2003). Making calculations from the data provided, fruit length:width ranged from 1.18-2.37 (average 1.57), length:weight from 12.96-37.57 g/mm (average 21.00) and width:weight from 8.92-19.14 g/mm (average 13.40). The current study showed considerably larger fruit size, length and width with a more restricted range of fruit length:width (same average), length:weight (lower average) and width:weight (lower average) than in Japan. Therefore, compared with the germplasm evaluated in Japan, the current study's larger, longer and wider Japanese genotypes were more moderately elongated and lower in density relating to both length and width.

Within the Japanese germplasm, the two heaviest fruit were also the longest and broadest, having the highest length:width and the lowest length:weight and width:weight. The four lightest Japanese genotypes were also some of the shortest and thinnest, having intermediate length:width and the highest length:weight and width:weight. Therefore, the heaviest Japanese fruit were not only longer and broader but denser, and the lightest Japanese fruit were not only shorter and thinner but less dense due to the three-dimensional nature of fruit size. Greater fruit weight was not directly associated with greater yield as the heaviest, largest genotypes were only intermediate yielding. The highest yielding genotypes had low to moderate weight, length and width. The heaviest, longest and broadest fruit had higher length:width, suggesting that fruit weight is not only associated with greater length and width but also a higher ratio between these two dimensions. Consequently, the largest fruit are longer and broader as well as more elongated.

There was promising variability for fruit agronomic potential in the Japanese germplasm especially regarding fruit yield and weight, the latter being most highly influenced by fruit length. High fruit weight was not a mandatory component of high yield within the Japanese group, but this group did have both higher yields and weight than the Kuril or Russian groups.

5.2.1.3 Kuril Foundation Germplasm

There were no significant differences in fruit yield between Kuril genotypes (**Table 5.1**; **Appendix C.1**). The four late (**Section 4.2.1**) genotypes had similar fruit weights (<1.00 g) equivalent to the smallest Japanese genotypes, but K-97-12 had significantly larger fruit (1.30 g), exceeding several smaller Japanese genotypes. The Kuril group's range in fruit weight was modest and was skewed due to inclusion of K-97-12. For fruit length, only K-97-12 was statistically different from the others (**Appendix C.2**). For fruit width, this genotype was wider than all other Kuril or Russian genotypes and thinner than only the two widest Japanese genotypes. The other four Kuril genotypes were thicker than all the Russian genotypes but only as wide as the two thinnest Japanese genotypes. There were no statistical differences in fruit length:width or length:weight for the Kuril group, but K-97-12 had significantly lower width:weight than the other four, which were not different from one another or from the three lowest ratios in the Russian group (**Appendix C.3**).

Overall, there was low variability for fruit agronomic potential in the Kuril germplasm. There are few references to Kuril germplasm in the literature, but Plekhanova (1992a) indicates

that Kuril germplasm has high yields and large fruit size in cold continental climates in Russia, which contrasts with the current findings in a temperate climate. Though greater fruit width:weight was a component of greater fruit weight, length and width, this was not related to higher yields.

5.2.1.4 Russian Foundation Germplasm

With significantly higher fruit yield than the rest of the Russian germplasm, R-27-35 (280.0 g) was statistically equivalent to the Kuril genotypes and some of the lower yielding Japanese genotypes (**Table 5.1**; **Appendix C.1**). R-2-13 (9.8 g) had significantly lower yield than the remaining intermediate Russian genotypes, which were statistically equivalent to one another. Russian fruit weights ranged from 0.61-0.96 g (average 0.75 g). Only two genotypes, R-2-06 and R-27-35, were as heavy as the four smaller Kuril genotypes, but none were as heavy as even the smallest Japanese genotype. Fruit length varied greatly from 14.76-22.92 mm (average 20.3 mm). R-2-13 and R-2-07 were statistically shorter and longer than all other genotypes, respectively, and there were no differences between the remaining Russian genotypes, which were equivalent to K-97-12 and intermediate Japanese genotypes (**Appendix C.2**). R-2-06, R-2-11 and R-27-35 were the broadest, whereas R-2-07 and R-2-16 were the thinnest.

Fruit length:width was lowest for R-2-13 and highest for R-2-07 (**Appendix C.3**). Fruit length:weight varied within the group, but all Russian genotypes had significantly greater ratios than any Kuril or Japanese genotype. R-2-07 had the highest ratio, followed by R-2-16 and R-2-10, while R-2-06, R-2-11 and R-27-35 had the lowest ratios. R-27-35 had statistically lower width:weight than all but R-2-06, and R-2-13 had a significantly higher ratio than all others.

The literature reports fruit yield ranges from 300-500 g in the third or fourth year in St. Petersburg (Plekhanova 1994b), 500-1,000 g in the fourth year in the Komi Republic (Ryabinina 2009), 240-780 g in the fourth to sixth years in Kamchatka (Petrushua 2009) and from 12-48 g and 450-1,069 g in the second and third years, respectively, in Poland (Ochmian and Grajkowsi 2007). Peak yields are reported between 2-5 kg from the seventh to fifteenth year in St. Petersburg (Plekhanova 1994b) and up to 3.2 kg in the fifth year in the Komi republic (Ryabinina 2009). Though the current study did not evaluate peak yield, very low yields for all Russian genotypes in early years in the Fraser Valley make it unlikely that they will reach the levels seen in cold climates when grown in temperate climates. This is validated by field observations of these trial plants in

2016, at which time they still had not reached yields of even 1.0 kg per plant when they should have reached their full potential.

Reports of Russian fruit weight range from 0.4-1.5 g in St. Petersburg (Plekhanova 2000), 0.70-1.35 g in Tschr (Bryksin 2009c), 0.4-1.3 g in the Komi Republic (Ryabinina 2009), 0.9-1.3 g in Barnaul (Khokhyrakova 2004), 0.78-1.11 g in Kamchatka (Petrushua 2009), 0.88-1.03 g in Poland (Ochmian and Grajkowski 2007) to 0.56-1.44 g in Romania (Ancu et al 2011). Russian selections are expected to have fruit weight between 1.1-1.4 g to be released as cultivars in St. Petersburg (Plekhanova 1994a) though 1.06-1.10 g is sufficient in the Mari El Republic (Golovunin 2009). Fruit length is reported from 17.0-28.7 mm and fruit width from 7.9-10.3 mm in Romania (Ancu et al 2011), while the former ranges from 10.0-17.0 mm in Russia (Kolasin and Pozdynakov 1991). Therefore, fruit weight, length and width in the Fraser Valley were within the general ranges reported from cold climates in Eurasia, but fruit weights were lower than the expectations for elite Russian cultivars in these regions.

At the U of S, replicated measurement of fruit weight, length and width, as well as ratings for productivity, included all Russian genotypes included in the current study except for R-27-35 (Bors et al 2012). Productivity ratings in Saskatchewan did not correlate with fruit yield or width measurements in the Fraser Valley ($r = 0.01$ and 0.04, respectively), but there were low and high correlations between respective measures of fruit weight and length ($r = 0.37$ and 0.82, respectively).

The lowest yielding genotype had light, short and narrow fruit with low fruit length:width, mediocre length:weight and high width:weight, meaning it was small and stout with low density. The highest yielding genotype had heavy, wide fruit that were only moderate in length and length:width but low in length:weight and width:weight. The next heaviest fruit was one of the broadest, but had moderate length, yield and length:width with low length:weight and width:weight. The next broadest fruit had moderate yield, weight, length:width and width:weight with low length:weight. The longest Russian fruit was also the narrowest and lightest with moderate yield and width:weight but the highest length:width and length:weight. Various combinations of fruit length and width interacted with apparent density to produce a range of fruit weights, but this only seems to related to yield at the high and low extremes. High yields were associated with heavy, broad fruit that were moderately elongated but with low apparent density. Therefore, temperate climate agronomic potential for the Russian germplasm was fundamentally

110

very low, and the associations between extremes in fruit yield and weight were connected to phenological adaptation rather than strict relationships between weight, length and width.

5.2.1.5 Out-group Comparisons to Foundation Germplasm

J-PP's yield was lower than the Japanese foundation group, weight was equivalent to the smallest of the Russian genotypes (**Appendix C.1**), length was equivalent to the shortest two Japanese genotypes and width was equivalent to average Russian genotypes (**Appendix C.2**). Its fruit length:width was matched only by one of the largest genotypes in the Japanese group and length:weight and width:weight were higher than all the Japanese and Kuril genotypes and some of the lower ratio Russian genotypes (**Appendix C.3**). These genotypes demonstrates less agronomic potential than the genotypes in the Japanese foundation group, which is directly related to its relatively early phenology.

'Borealis' (68.7 g/plant and 1.05 g/fruit), 'Tundra' (66.3 g/plant and 1.01 g/fruit) and 'Indigo Gem' (126.4 g/plant and 1.04 g/fruit) had statistically equivalent fruit yields and weights. Their yields were all lower than the Japanese and Kuril genotypes but higher than all Russian genotypes, except R-27-35 for all three cultivars as well as R-2-07 for 'Tundra'. Their average weights were greater than all Russian genotypes except R-27-35, equivalent to the four smaller Kuril genotypes and the two smallest Japanese genotypes but smaller than K-97-12, their maternal genotype. 'Borealis' was shorter and thinner than 'Indigo Gem', which was shorter but not thinner than the more intermediate 'Tundra'. Fruit lengths were equivalent to the short and intermediate Japanese genotypes and longest Kuril genotypes. All three were longer than R-2-13, but only 'Tundra' was equal in length to R-2-11, the next shortest Russian genotype. They were broader than any Russian genotype, equivalent to the narrowest Japanese genotypes and either equivalent to ('Borealis' and 'Tundra') or broader than ('Indigo Gem') the various late Kuril genotypes. All three were shorter and thinner than K-97-12.

'Borealis' and 'Indigo Gem' had equivalent fruit length:width and length:weight but had lower ratios than 'Tundra', while width:weight was the same for all three cultivars. Consequently, 'Borealis' and 'Indigo Gem' length:width and length:weight were equivalent to all Kuril genotypes, and 'Tundra' length:width was higher than all Kuril genotypes and length:weight was higher than K-97-12 but not the rest of the Kuril group. 'Borealis' width:weight was equivalent to the highest Japanese, all the Kuril group and the two lowest Russian ratios. 'Tundra' and 'Indigo

111

Gem' had significantly higher ratios than most Japanese genotypes and K-97-12 but were equivalent to the four late Kuril genotypes and low to intermediate Russian genotypes.

Evaluations at the U of S describe 'Borealis' as the largest of these three cultivars (1.62 g/fruit), 'Tundra' as slightly smaller (1.49 g) and 'Indigo Gem' as smaller still (1.3 g) (Bors et al 2009). These values are greater than for the Russian genotypes that had a range from 0.6-1.05 g (Bors et al 2012). Biologically replicated measurement of fruit weight in the Fraser Valley showed no statistical differences in fruit weight between the U of S cultivars but lower averages than measured in Saskatchewan. As hybrids of Kuril and Russian parents, these cultivars were selected in a cold climate and do not demonstrate comparable agronomic potential to even the low end of the Japanese group in a temperate climate. This finding relates to their lack of phenological adaptation (**Section 4.2.1**).

5.2.1.6 Correlations between Fruit Morphological Traits

Across foundation groups, positive correlations were seen between fruit yield, weight, length and width. Yield had high and moderate correlations with weight and width, respectively; weight had very high and low correlations with width and length, respectively; and length had low correlations with weight and width (**Table 5.2**). There was no significant correlation between yield and length. For the Japanese group, correlations were low for yield with weight and width, while they were high for weight with length and width and for length with width. For the Kuril group, correlations were low for yield with weight, but high and moderate for weight with length and width, respectively, and high for length with width. For the Russian group, correlations were moderate for yield with weight, length and width, whereas they were low and high for weight with length and width, respectively.

Across foundation groups, yield, weight and width were negatively correlated with fruit length:width, length:weight and width:weight, especially the latter two ratios. In contrast, fruit length had a low negative correlation with width:weight, a positive correlation with length:width and no correlation with length:weight. There were high positive correlations between length:weight and both length:width and width:weight. For the Japanese group, length:width was only correlated with length, but correlations with length:weight ranged from low with length, moderate with yield and width to high with weight. Width:weight had similar correlations or stronger based on its high correlation with length:weight. For the Kuril group, correlations were

Table 5.2. Foundation Germplasm: Pearson's correlations between fruit morphological traits for blue honeysuckle in 2012/2013 in the Fraser Valley, BC, Canada (only statistically significant correlations [p < 0.05] are shown).

Block 1:

		Group	r
Yield	Weight	All	0.719
		Japanese	0.464
		Kuril	0.455
		Russian	0.681
	Length	Russian	0.620
	Width	All	0.640
		Japanese	0.382
		Russian	0.505
	Length:Width	All	-0.301
	Length:Weight	All	-0.662
		Japanese	-0.500
		Kuril	-0.622
		Russian	-0.339
	Width:Weight	All	-0.707
		Japanese	-0.490
		Kuril	-0.651
		Russian	-0.633
Weight	Length	All	0.491
		Japanese	0.776
		Kuril	0.789
		Russian	0.476

Block 2:

		Group	r
Weight	Width	All	0.901
		Japanese	0.895
		Kuril	0.661
		Russian	0.792
	Length:Width	All	-0.335
		Kuril	0.326
	Length:Weight	All	-0.852
		Japanese	-0.894
		Kuril	-0.819
		Russian	-0.802
	Width:Weight	All	-0.942
		Japanese	-0.961
		Kuril	-0.858
		Russian	-0.875
Length	Width	All	0.402
		Japanese	0.728
		Kuril	0.802
	Length:Width	All	0.572
		Japanese	0.605
		Kuril	0.464
		Russian	0.739

Block 3:

		Group	r
Length	Length:Weight	Japanese	-0.436
	Width:Weight	All	-0.480
		Japanese	-0.702
		Kuril	-0.436
		Russian	-0.490
Width	Length:Width	All	-0.491
		Russian	-0.464
	Length:Weight	All	-0.795
		Japanese	-0.785
		Russian	-0.700
	Width:Weight	All	-0.736
		Japanese	-0.772
		Russian	-0.455
Length:Width	Length:Weight	All	0.722
		Russian	0.637
	Width:Weight	Kuril	-0.513
Length:Weight	Width:Weight	All	0.816
		Japanese	0.902
		Kuril	0.887
		Russian	0.668

moderate between yield and length:weight, high between weight and width:weight, low between length:width and width:weight, whereas they were moderate and high for width:weight with length:width and length:weight, respectively. For the Russian group, length:width had contrasting low negative and high positive correlations with width and length, respectively. Negative correlations were high and low for length:weight with width and yield, respectively, and high and moderate for width:weight with weight and length, respectively; however, moderate positive correlations were detected for length:weight with length:width and width:weight.

Therefore, across foundation groups, fruit yield was correlated with weight and, to a less degree, with width. The same was true for fruit weight with length and width, the latter being stronger than the former. There was also a low correlation between length and width across foundation groups. Elongated fruit (i.e., higher length:width) had greater length and lower yields and weights as well as density relative to length but not width. Low density relative to length (i.e., high length:weight) was associated with lower yield and weight, but these relationships were even stronger for density relative to width (i.e., high width:weight). Therefore, as a major driver of yield, fruit weight is primarily determined by width and secondarily by length. This is shown by the negative relationship between weight and length:width and the fact that weight has a stronger relationship with density relative to width than density relative to length.

Within foundation groups, there were correlations between fruit yield and weight, though not as strong as across the germplasm. Only the Russian group showed correlations for yield with both length and width. The Japanese group had a low correlation between yield and width, but the Kuril group did not demonstrate sufficient variation in these variables for a significant correlation to materialize. The correlations between weight and length were higher in each foundation group on its own than across the germplasm, whereas the opposite was true regarding weight and width. Similarly, the low correlation between length and width across the germplasm was high for the Japanese and Kuril groups on their own and non-significant for the Russian group on its own. Yield and width were more strongly correlated with weight across the germplasm than within each foundation group, and length and weight were more strongly related within groups than across the germplasm. While all groups had correlations between yield and weight, correlations between length and width in the Japanese and Kuril groups set them apart from the Russian group, which had a correlation between length and yield instead. Stronger correlations for weight with both length and width in Japanese and Russian groups set them apart from the Kuril group.

114

Correlations between fruit morphological traits varied in importance across the germplasm and within foundation groups, demonstrating the complexity of agronomic potential in blue honeysuckle. Length:width were more strongly correlated with length within the Russian group than across the germplasm, which was similar to the Japanese group and stronger than for the Kuril group. The low correlations between length:width and yield and between weight and width across the germplasm were not of fundamental importance within groups. Correlations for length:weight with both yield and weight were similar across the germplasm as within groups, but a low negative correlation between length:weight and length within the Japanese group was not seen in the other two groups or across the germplasm. Equally, high correlations between length:weight and width were seen in both the Japanese and Russian groups but not the Kuril group or the germplasm as a whole. Width:weight was correlated with yield and weight in each foundation group but not as strongly as across the germplasm. Width:weight was correlated more strongly with length and width in the Japanese group than the Kuril or Russian groups, the germplasm as a whole showing a similar correlation to these latter groups for length and to the former group for width.

Since blue honeysuckle fruit are three-dimensional objects, the relationships between size parameters (i.e., weight, length and width) and their ratios (i.e., length:width, length:weight and width:weight) are complex. The current study shows differences across and within genetic groups in the relative rates at which size parameters increase or decrease. These differences in phenotype relate to genetic differences in the rates of increase in different planes, ratios between dry matter and juice content, heterogeneity and irregularity of fruit shapes.

5.2.2 Quantitative Measures of Agronomic Potential in Improved Germplasm
5.2.2.1 Parent Genotype Contrasts for Improved Germplasm Families

The Japanese and Kuril parents did not have significantly different fruit yield for seven of eight Japanese/Kuril families, but the Japanese parent was significantly higher yielding in one family (**Appendix C.4**). The Japanese parent had significantly higher fruit weight, length and width for seven families and the Kuril parent for the remaining family. Five families showed no difference in length:width, while the Japanese and Kuril parent had higher ratios in two and one families, respectively. The Kuril parent had higher length:weight and width:weight for seven families, the remaining showing no difference. The Japanese parent had higher yield for half the families, though the other half showed no differences for the 16 Japanese/Russian families. The

Japanese parent had significantly higher fruit weight and width and the Russian parent had higher length:weight and width:weight. The Japanese and Russian parents had longer fruit for seven and three families, respectively, and six showed no significant difference. The Russian parent had a higher length:width for 13 families, the Japanese parent for two families, there was no difference between parents in the remaining family. The Kuril parent had higher yield, weight and width for six, eleven and twelve Kuril/Russian families, respectively, the remaining showing no difference. In contrast, there were 11 families with a longer Russian parent, four with a longer Kuril parent and one with no difference. The Russian parent had higher length:width, length:weight and width:weight for 13, 14 and 12 families, respectively, the rest showing no difference.

5.2.2.2 Absolute Range, Group Extremes and Heritability

The lowest fruit yield (29.4 g), weight (0.55 g) and length (15.1 mm) were in the Kuril/Russian group (**Figure 5.3**; **Table 5.3**). The lowest Japanese/Kuril and Japanese/Russian yields were much higher (329.4 and 357.4 g, respectively). The lightest Japanese/Russian and Japanese/Kuril fruit were nearly as small (0.60 g) and noticeably heavier (1.00 g), respectively. The shortest Japanese/Kuril (15.5 mm) and Japanese/Russian extremes (15.7 mm) were nearly as short. The narrowest fruit (8.8 mm) were in the Japanese/Russian group, followed closely by the Kuril/Russian group (9.0 mm) and more distantly by the Japanese/Kuril group (11.2 mm). The highest yield (1,834.2 g) and length (29.7 mm) were in the Japanese/Kuril group, and the heaviest (2.06 g) and broadest (14.9 mm) fruit were in the Japanese/Russian group. The highest Japanese/Russian and Kuril/Russian yields (1,703.4 and 1,706.3 g) and length (26.3 and 27.1 mm) were not far behind. The heaviest Kuril/Russian (1.70 g) was further behind than the Japanese/Kuril extreme (1.94 g), but neither the Japanese/Kuril nor Kuril/Russian group were far behind in maximum width (13.9 and 14.2 mm, respectively).

The lowest fruit length:width (1.17) and width:weight (11.5 mm/g) were in the Japanese/Kuril group, followed by Japanese/Russian (1.29 and 7.1 mm/g) and Kuril/Russian (1.47 and 8.5 mm/g) groups (**Figure 5.4**; **Table 5.4**). The lowest length:weight (6.6 mm/g) was a Japanese/Russian genotype, the Japanese/Kuril group having nearly as low an extreme (12.9 mm/g) and the Kuril/Russian group a considerably less pronounced extreme (15.0 mm/g). The highest length:width (2.74), length:weight (33.6 mm/g) and width:weight (17.0 mm/g) were in the
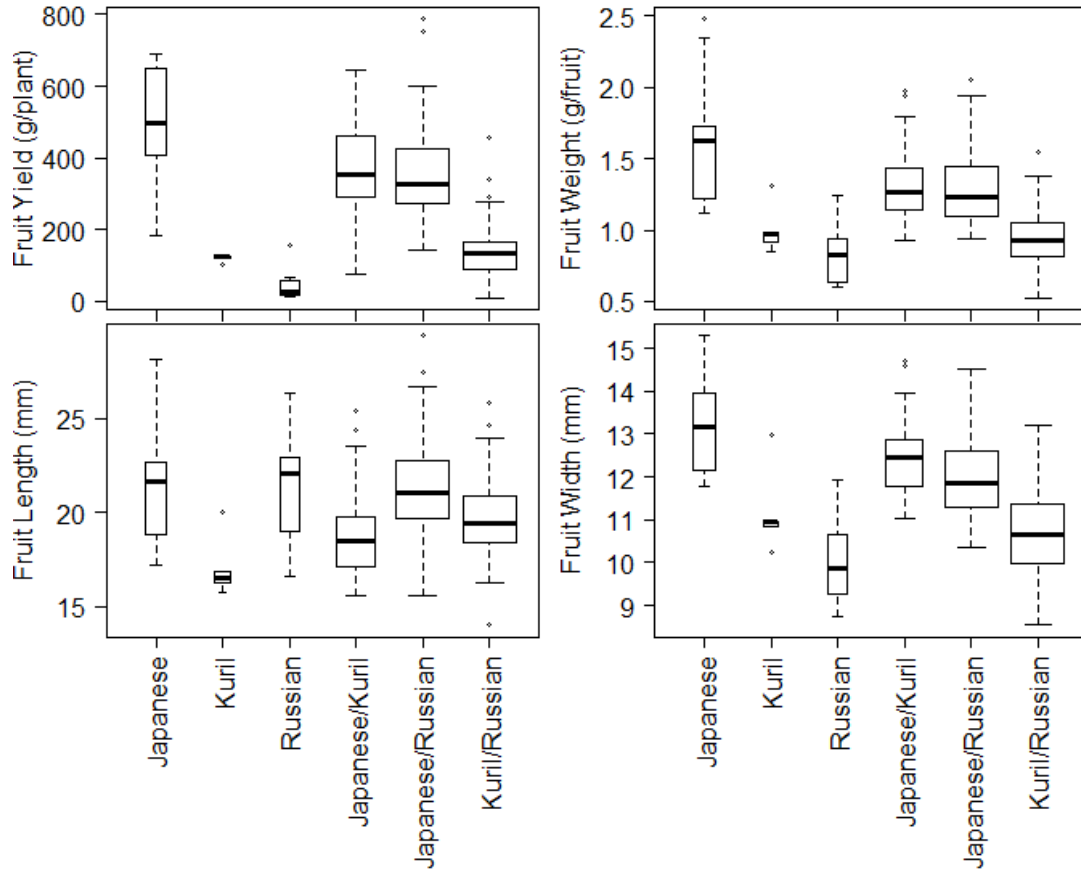
Figure 5.3. Foundation and Improved Germplasm: Fruit morphological features in blue honeysuckle evaluated in 2012/2013 in Chilliwack, BC, Canada (boxplot widths are proportional to the square root of the sample size for each group).

Table 5.3. Foundation and Improved Germplasm: Fruit morphological features in blue honeysuckle in 2012/2013 in Chilliwack, BC, Canada.

Group	Japanese	Kuril	Russian	Japanese/ Kuril	Japanese/ Russian	Kuril/ Russian
Fruit Yield (g/plant)						
Average	1147.8	986.7	744.0	1157.5	999.4	1002.0
Median	1099.1	986.4	760.1	1215.1	1004.2	1041.1
Minimum	620.7	805.5	114.0	329.4	357.4	29.4
Maximum	1552.1	1132.8	1164.7	1834.2	1703.4	1706.3
Range	931.3	327.3	1050.7	1504.8	1346.0	1676.9
Fruit Weight (g/fruit)						
Average	1.64	1.01	0.84	1.32	1.23	1.10
Median	1.63	0.96	0.85	1.29	1.15	1.12
Minimum	1.14	0.87	0.61	1.00	0.60	0.55
Maximum	2.49	1.35	1.25	1.94	2.06	1.70
Range	1.35	0.49	0.64	0.94	1.46	1.14
Fruit Length (mm)						
Average	21.63	17.18	21.68	19.82	20.07	21.40
Median	21.65	16.45	22.45	19.01	19.63	21.17
Minimum	17.29	15.84	16.28	15.54	15.75	15.12
Maximum	28.33	20.29	26.33	29.70	26.26	27.11
Range	11.04	4.46	10.05	14.16	10.51	11.98
Fruit Width (mm)						
Average	13.22	11.22	10.16	12.25	12.00	11.19
Median	13.15	10.98	10.15	12.21	11.79	11.24
Minimum	11.84	10.27	8.78	11.19	8.79	9.00
Maximum	15.25	13.05	11.93	13.86	14.88	14.25
Range	3.41	2.78	3.15	2.66	6.09	5.25
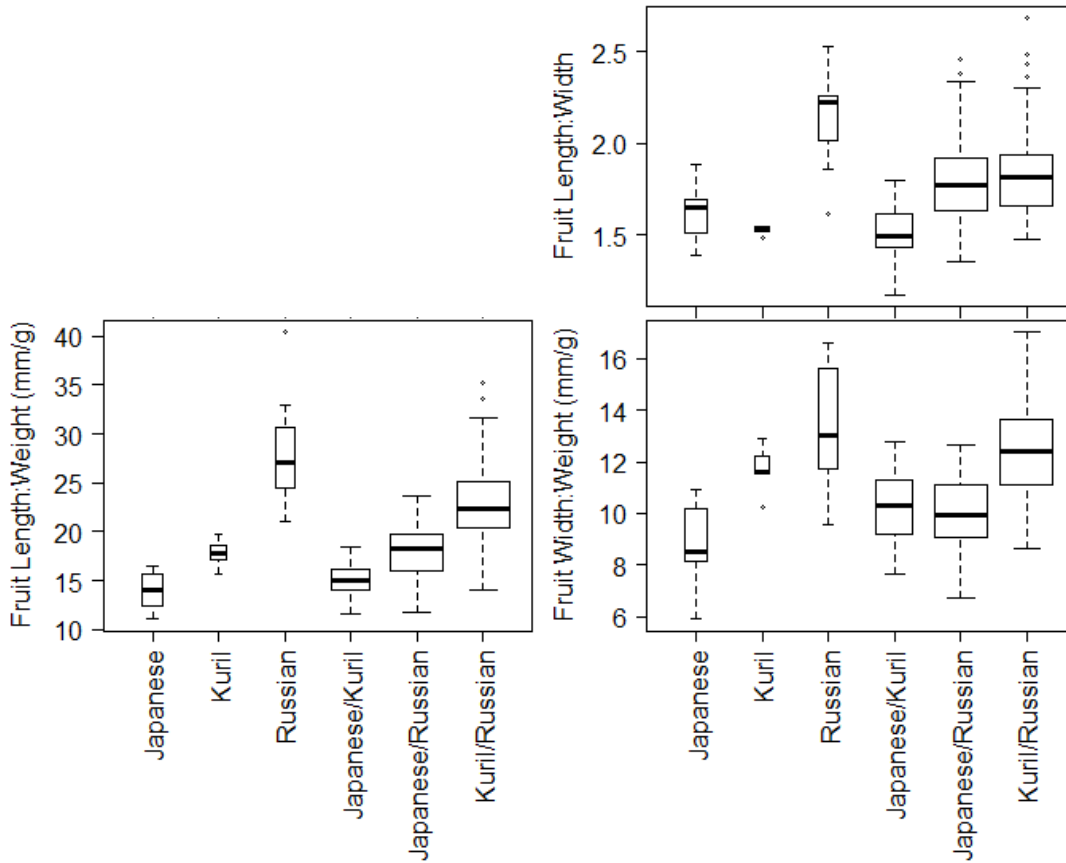
Figure 5.4. Foundation and Improved Germplasm: Ratios between fruit morphological features in blue honeysuckle evaluated in 2012/2013 in Chilliwack, BC, Canada (boxplot widths are proportional to the square root of the sample size for each group).

Table 5.4. Foundation and Improved Germplasm: Ratios between fruit morphological features in blue honeysuckle in 2012/2013 in Chilliwack, BC, Canada.

Group	Japanese	Kuril	Russian	Japanese/ Kuril	Japanese/ Russian	Kuril/ Russian
Fruit Length:Width						
Average	1.6	1.5	2.2	1.6	1.7	1.9
Median	1.7	1.5	2.2	1.6	1.7	1.9
Minimum	1.4	1.5	1.6	1.2	1.3	1.5
Maximum	1.9	1.6	2.5	2.5	2.2	2.7
Range	0.5	0.1	1.0	1.3	0.9	1.3
Fruit Length:Weight (mm/g)						
Average	13.87	17.71	27.95	15.62	17.98	21.06
Median	14.11	17.60	26.83	15.17	17.49	20.73
Minimum	11.07	15.36	21.10	12.93	11.51	14.97
Maximum	16.39	19.41	39.42	19.70	30.89	33.56
Range	5.32	4.06	18.32	6.76	19.37	18.60
Fruit Width:Weight (mm/g)						
Average	8.69	11.63	13.20	9.86	10.74	11.09
Median	8.49	11.77	12.69	9.83	10.68	10.69
Minimum	5.88	10.00	9.56	6.60	7.07	8.53
Maximum	10.74	12.62	17.08	11.83	15.71	17.00
Range	4.85	2.62	7.52	5.23	8.64	8.47

Kuril/Russian group, the highest Japanese/Russian extremes following close behind (2.46, 30.9 mm/g and 15.7 mm/g) with the highest Japanese/Kuril extreme following considerably further behind (2.21 19.7 mm/g and 11.8 mm/g).

The highest and lowest values for yield and length were in the Japanese/Kuril and Kuril/Russian groups, respectively, resulting in ranges for the improved germplasm (1,804.8 g and 14.6 mm) that completely overlapped the more restricted ranges in the foundation germplasm (1,438.1 g and 12.5 mm). In contrast, the overall range in weights (1.94 g) was wider than for either the improved (1.51 g) or foundation (1.62 g) germplasm because the heaviest and lightest extremes were in the Japanese and Kuril/Russian group, respectively. The overall range in widths (6.5 mm) was the same as the foundation germplasm but more extensive than for the improved germplasm (6.1 mm) as the widest and narrowest extremes were Japanese and Russian genotypes, respectively.

The absolute ranges for all four variables were wider in the Japanese/Russian and Kuril/Russian groups than in any of their respective parent groups, except that the range in Japanese/Russian length was not as great as in the Japanese group. In contrast, the Japanese/Kuril group had more extensive ranges for yield and length than its parent groups, a broader range for weight than only the Kuril group and a more restricted range for width than either of its parent group. The highest and lowest yields in the Japanese/Kuril and Kuril/Russian groups, respectively, relate to the high, moderate and low yields observed in the Japanese, Kuril and Russian foundation groups, respectively. Similarly, the greater weights seen in the Japanese/Kuril and Japanese/Russian groups compared to the Kuril/Russian group was expected based on the much larger average fruit size in the Japanese group than in the Kuril or Russian groups. The longest improved genotypes had a short Kuril parent, whereas the less extreme Japanese/Russian group had the longest parent groups. Improved germplasm extremes overlapped the thinnest/broadest Kuril but not Japanese genotypes (Japanese/Kuril), the thinnest Japanese and broadest Russian genotypes (Japanese/Russian) and the thinnest/broadest Kuril and only the broadest Russian genotypes (Kuril/Russian).

For length:width, the Japanese/Kuril and Kuril/Russian groups completely overlapped their respective parent groups, but the Japanese/Russian group did not overlap the high Russian group extreme. For length:weight, the Japanese/Kuril group surpassed all but the high Kuril group extreme and the Kuril/Russian group topped all but the high Russian group extreme. However,

the Japanese/Russian group only overlapped the high Japanese and low Russian group extremes. For width:weight, the Japanese/Kuril group exceeded only the low Japanese and high Kuril group extremes; the Japanese/Russian group surpassed only the low Russian and high Japanese group extremes; and the Kuril/Russian group overlapped the low extremes of both groups but only the high Russian group extreme. For length:width, the Japanese/Kuril and Kuril/Russian groups had broader ranges than any foundation group, but the Japanese/Russian group's range was as broad as that of the Russian group. For length:weight and width:weight, the improved groups had broader ranges than either the Japanese or Kuril groups. Only the Japanese/Russian group had a wider range than the Russian group for length:weight, whereas both the Japanese/Russian and Kuril/Russian groups had broader ranges for width:weight.

In comparison, for 100 advanced selections made from improved germplasm at the U of S in a cold continental climate in Saskatchewan, weight varied from 1.1-3.4 g (average 1.9), length from 16.3-32.0 mm (average 24.8) and width from 10.8-15.4 mm (average 12.7) (Bors et al 2015). Calculating ratios from this data, length:width ranged from 1.19-2.57 (average 1.97), length:weight from 8.61-18.41 g/mm (average 13.32) and width:weight from 4.11-9.65 g/mm (average 6.87). Therefore, in the Fraser Valley, the improved groups showed a slightly narrower range and lower average weight but nearly as extensive a range in length and width with slightly more restricted overall ranges and lower averages than in Saskatchewan. In contrast, in the current study, length:width had a slightly broader range and length:weight and width:weight had broader ranges and higher averages.

For fruit yield, weight and length, H^2 was moderate, whereas it was high for fruit width for the foundation and improved germplasm combined; moderate for yield, high for weight and length and very high for width for the foundation germplasm on its own; and low for yield, moderate for weight and length and high for width for the improved germplasm on its own (**Table 5.5**). H^2 was moderate to high for yield, weight, length and width in the Japanese group, varying considerably for the Kuril group from negligible to very high and being negligible to low for the Russian group. H^2 was low to high in the Japanese/Kuril group and low to moderate for the other improved groups. Across the foundation and improved germplasm combined or separate, H^2 was lowest for yield, highest for fruit width and more moderate for weight and length. This same general trend was seen in each improved group on its own as well as the Japanese and Kuril foundation groups on their own but not in the Russian group, which demonstrated the opposite trend. In the foundation

122

Table 5.5. Foundation and Improved Germplasm: Heritability estimates for fruit morphological traits in blue honeysuckle in 2012/2013 in Chilliwack, BC, Canada (H^2 – broad-sense heritability calculated from linear mixed model regression, h^2 – narrow-sense heritability calculated from mid-parent regression on phenotypic averages[1]).

	Fruit Yield		Fruit Weight		Fruit Length		Fruit Width		Fruit Length: Width		Fruit Length: Weight		Fruit Width: Weight	
	H^2	h^2	H^2	h^2	H^2	h^2	H^2	h^2	H^2	h^2	H^2	h^2	H^2	h^2
All Germplasm	0.50	-	0.64	-	0.56	-	0.77	n/a	0.87	-	0.80	-	0.53	-
All Foundation	0.60	-	0.84	-	0.76	-	0.91	n/a	0.94	-	0.91	-	0.73	-
Japanese	0.57	-	0.77	-	0.80	-	0.88	n/a	0.76	-	0.73	-	0.64	-
Kuril	0.00	-	0.50	-	0.74	-	0.92	n/a	0.00	-	0.24	-	0.17	-
Russian	0.45	-	0.33	-	0.44	-	0.15	n/a	0.94	-	0.36	-	0.30	-
All Improved	0.49	0.49	0.58	0.61	0.53	0.63	0.74	0.45	0.85	0.27	0.77	0.47	0.49	0.45
Japanese/Kuril	0.36	0.28	0.57	0.41	0.65	0.76	0.74	0.53	0.74	0.17	0.51	0.41	0.42	0.41
Japanese/Russian	0.37	0.00	0.49	0.00	0.50	0.38	0.69	0.23	0.79	0.00	0.64	0.23	0.35	0.41
Kuril/Russian	0.38	0.00	0.39	0.00	0.38	0.11	0.53	0.28	0.87	0.30	0.56	0.15	0.34	0.00

[1]Different regression models were used to calculate H^2 and h^2 heritability estimates, so these measures are not directly comparable.

germplasm, the Japanese group had the highest H^2 for yield, weight and length, while the Kuril group had the highest H^2 for width. H^2 was negligible for yield in the Kuril group and width in the Russian group. In the improved germplasm, aside from yield, which was low across the board, H^2 for weight, length and width was highest in the Japanese/Kuril group, followed by the Japanese/Russian and then the Kuril/Russian group. Fruit weight had higher H^2 than length, which was higher than for width.

Compared to their parent groups, H^2 for the Japanese/Kuril group was intermediate for yield and weight and lower for length and width. For the Japanese/Russian group, H^2 was lower for yield and intermediate for weight, length and width. For the Kuril/Russian group, H^2 was intermediate for yield, weight and width but lower for length. Thus, H^2 for yield was intermediate between parent groups for the Japanese/Kuril and Kuril/Russian groups but lower for the Japanese/Russian group. For weight, H^2 was intermediate for all three improved groups, and for length it was intermediate for the Japanese/Russian group and lower for the other improved groups. For width, H^2 was lower than for both parent groups for the Japanese/Kuril group and intermediate for the other groups.

In comparison, h^2 was moderate for all four variables across the improved germplasm and in the Japanese/Kuril group on its own, but only substantial for weight and length in the Japanese/Russian group and for length in the Kuril/Russian group. h^2 was higher for yield and weight than for length and width across the improved germplasm. The Japanese/Kuril group had higher h^2 for weight than width, which was higher than for length and yield. The Japanese/Russian group had higher h^2 for weight than for length. The Kuril/Russian group only showed any considerable h^2 for length.

For length:width, length:weight and width:weight, H^2 was moderate to high across the foundation and improved germplasm combined, and it was high to very high for the foundation germplasm on its own and low for the improved germplasm on its own. It was moderate to high for the Japanese group and negligible for the Kuril group, varying considerably from negligible to very high for the Russian group and from low to high for the improved groups individually.

Across the foundation and improved germplasm, H^2 was highest for length:width followed by length:weight and somewhat lower for width:weight. This same overall trend was seen across the foundation germplasm alone, the improved germplasm alone and in each improved group individually. In the foundation groups, H^2 was slightly higher for length:width and length:weight

than width:weight in the Japanese group; negligible for each ratio in the Kuril group; and much higher for length:width than length:weight or length:width in the Russian group. Across ratios, the Russian group had the highest H^2 for length:width, and the Japanese group had the highest H^2 for length:weight and width:weight. In the improved groups, H^2 for length:width was highest in the Kuril/Russian group but not much lower in the other groups. For length:weight, H^2 was highest in the Japanese/Russian group, followed closely by the Kuril/Russian and then Japanese/Kuril group. For width:weight, H^2 was only slightly higher in the Japanese/Kuril group than the other two groups.

Compared with their parent groups, H^2 for the Japanese/Kuril and Japanese/Russian groups was intermediate for all three ratios. In contrast, for the Kuril/Russian group, H^2 was only intermediate for length:width, which was much closer to the very high H^2 of the Russian group than the negligible H^2 of the Kuril group. For length:weight and width:weight, H^2 in the Kuril/Russian group was higher than in either the Kuril or Russian group, where H^2 was negligible for the former in the Kuril group two ratios and for the latter in the Russian group. In other words, H^2 for length:width was intermediate between parental foundation groups for all improved groups. In contrast, length:weight and width:weight had intermediate H^2 for the Japanese/Kuril and Japanese/Russian groups, though it was higher than either parental group for the Kuril/Russian group.

Across the improved germplasm, h^2 was low to moderate for the three ratios. It was negligible to moderate for the Japanese/Kuril and Japanese/Russian groups and low in the Kuril/Russian group for length:width alone. Consequently, h^2 was highest for length:weight and then width:weight, while it was lowest for length:width across the improved groups. It was higher for length:width in the Kuril/Russian group and for length:weight in the Japanese/Kuril, but equal for width:weight in the Japanese/Kuril and Japanese/Russian groups.

5.2.2.3 Improved Japanese/Kuril Germplasm

The Japanese/Kuril group ranged in yield from 329.4-1,834.2 g/plant, weight from 1.00-1.94 g/fruit, length from 15.5-29.7 mm and width from 11.2-13.9 mm (**Table 5.3**). The distribution of observations for yield showed a bimodal pattern more like that of the Japanese than the Kuril group. In contrast, for weight, length and width, distributions were largely intermediate between the parent groups. Compared to the Japanese group, the ranges in yield and length were two thirds

125

and one third greater, respectively, whereas the ranges in weight and width were half as much and slightly lower, respectively. In comparison with the Kuril group, the ranges in yield, weight and length were four, two and three times greater, but width was similar in range.

The low and high extremes in yield and length completely overlapped the extremes for both parent groups. For weight and width, the low extremes overlapped the Japanese but not the Kuril group and the opposite for the high extremes. For yield, there were similarly low proportions of low and high transgressive segregants as well as low and high-parent types, leaving a full three quarters as intermediates (**Figure 5.5**; **Appendix C.5**). For weight and length, there were more high transgressive segregants and high-parent types than low, and there was a minority of intermediates. For width, although there was only one low transgressive segregants and no high transgressive segregants, there were far more low-parent types than high with intermediates comprising half.

Range in fruit length:width was from 1.17-2.46, length:weight from 12.9-19.7 mm/g and width:weight from 6.6-11.8 mm/g (**Table 5.4**). For length:width, the distribution was skewed lower than either parent group, stretching across the ranges of each. For length:weight and width:weight, the distributions were intermediate between those of the parent groups. Compared with the Japanese group, the range was twice as broad for length:width and only slightly larger for length:weight and width:weight. Contrasted against the Kuril group, the range was many times wider for length:width, slightly larger for length:weight and twice as large for width:weight.

The extremes for length:width overlapped those of both parent groups. In contrast, the low extreme did not overlap that of the Japanese group for either length:weight or width:weight, the high extreme not overlapping that of the Kuril group for the latter ratio. For length:width, while low-parent types far outnumbered high, there were about the same number of low transgressive segregants as high, leaving a small portion of intermediates (**Figure 5.5**; **Appendix C.5**). For length:weight and width:weight, there were some low transgressive segregants and few to no high transgressive segregants, but there were far more low-parent types than high and only a minority of intermediates.

The Japanese/Kuril group showed primarily additive gene action for yield with a low degree of transgressive segregation and very little skew; a moderate proportion of additive gene action for width and a slight skew toward dominance, but not overdominance, of narrower Kuril fruit; low degrees of additive gene action for weight and length with higher proportions of
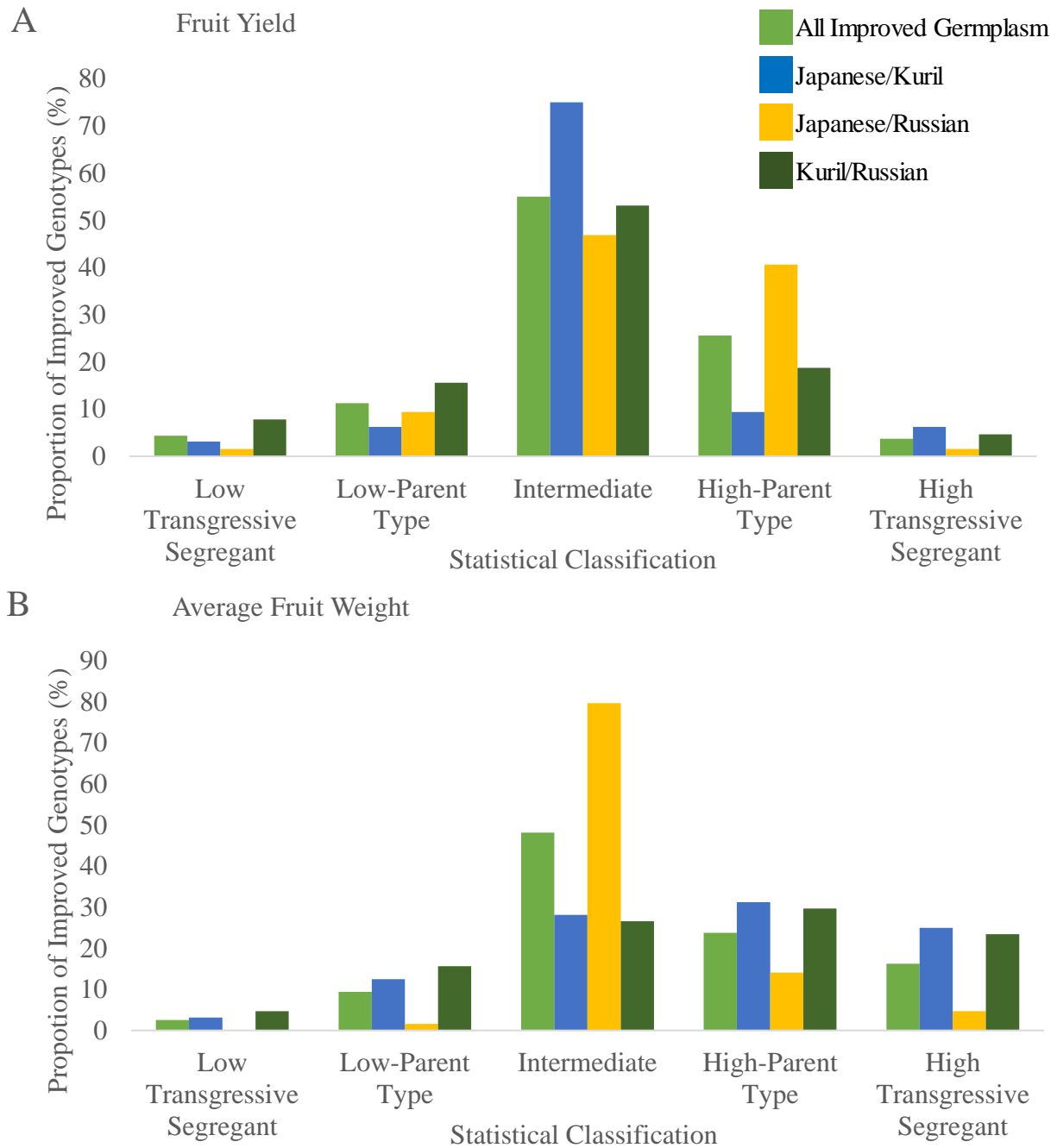
Figure 5.5. Improved Germplasm: Statistical classification of blue honeysuckle hybrids compared to their parent genotypes for fruit morphology in 2012/2013 in Chilliwack, BC, Canada (A) Yield (B) Weight (C) Length (D) Width (E) Length:width (F) Length:weight (G) Width:weight.
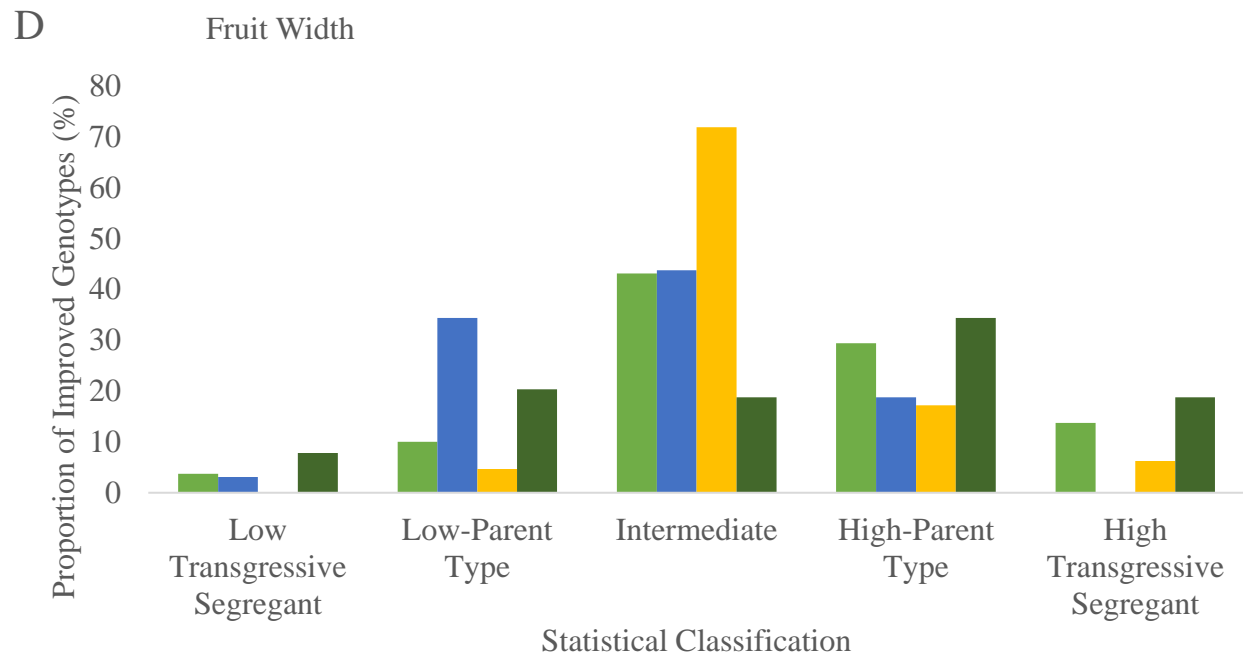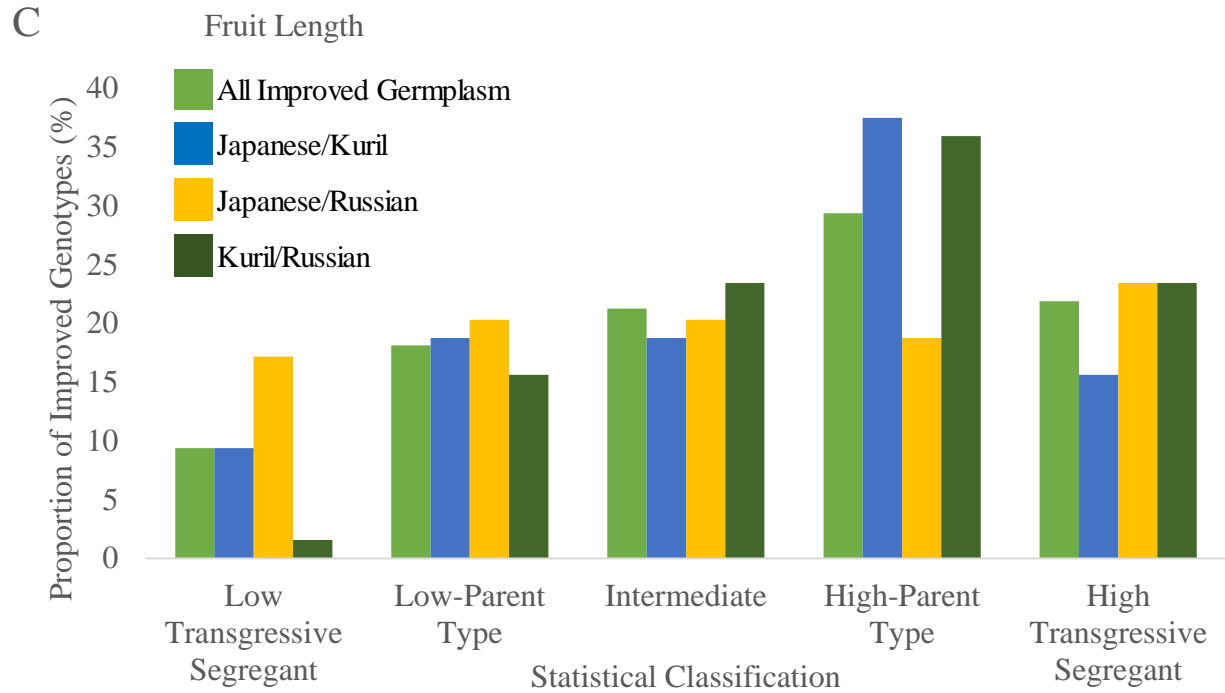
Figure 5.5. Continued. Improved Germplasm: Statistical classification of blue honeysuckle hybrids compared to their parent genotypes for fruit morphology in 2012/2013 in Chilliwack, BC, Canada (A) Yield (B) Weight (C) Length (D) Width (E) Length:width (F) Length:weight (G) Width:weight.

128
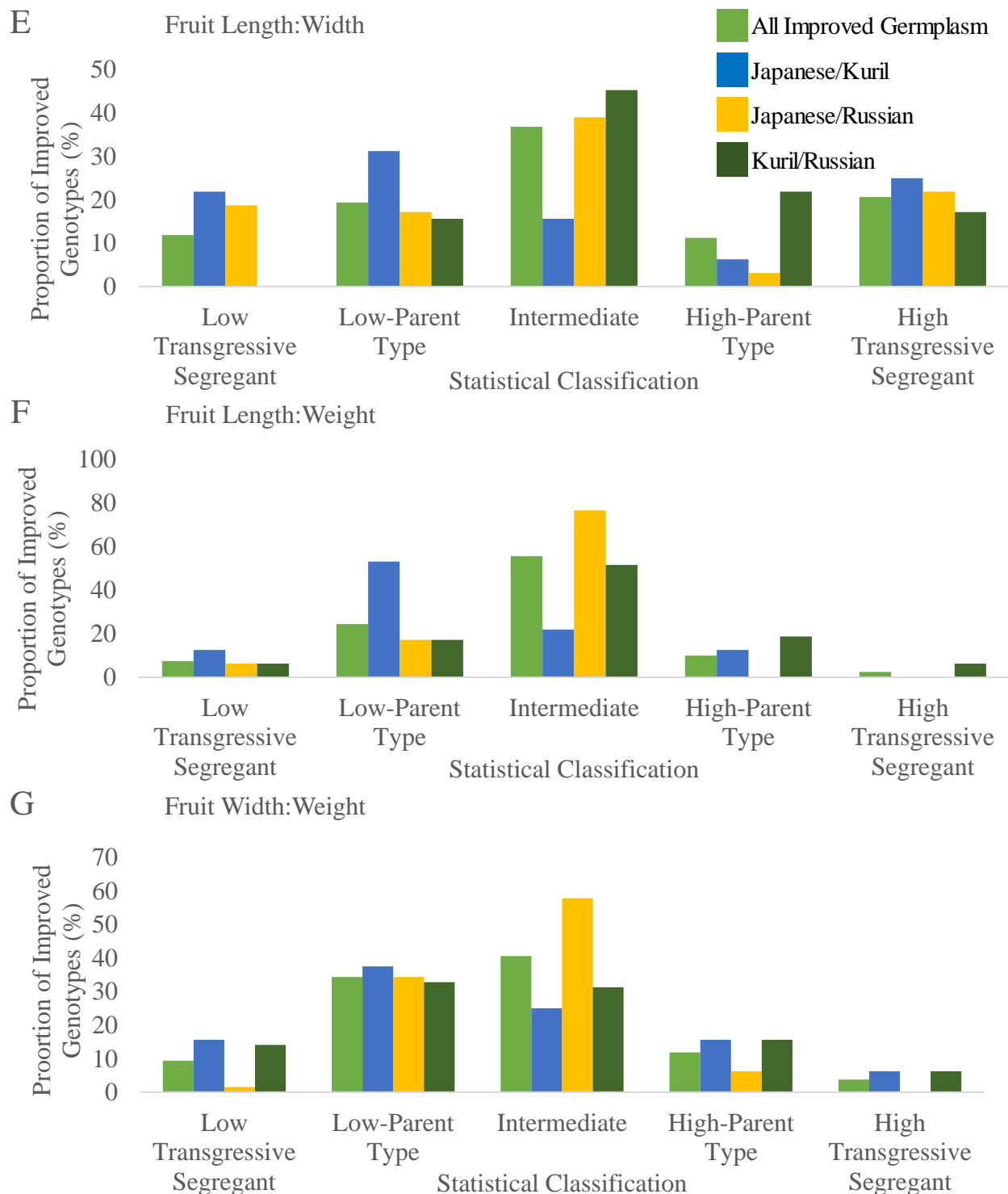
Figure 5.5. Continued. Improved Germplasm: Statistical classification of blue honeysuckle hybrids compared to their parent genotypes for fruit morphology in 2012/2013 in Chilliwack, BC, Canada (A) Yield (B) Weight (C) Length (D) Width (E) Length:width (F) Length:weight (G) Width:weight.

transgressive segregation that were considerably skewed toward dominance and overdominance of heavier, longer Japanese fruit; a low proportion of additive gene action but considerable dominance of low length:width from either parent and overdominance in both directions; and little additive gene action, but substantial dominance and some overdominance, of low length:weight and width:weight from the Japanese parent.

5.2.2.4 Improved Japanese/Russian Germplasm

The Japanese/Russian group ranged in yield from 357.4-1,703.4 g/plant, weight from 0.60-2.06 g/fruit, length from 15.7-26.3 mm and width from 8.8-14.9 mm (**Table 5.3**). The distribution for yield was bimodal, with high and low peaks that bore similarities to both the Japanese and Russian groups. For weight and width, the distributions were intermediate between the two parent groups. However, the distribution was much closer to that of the Japanese group for length. Contrasting with the Japanese group, the absolute ranges in yield and width were half again and twice as large, while for weight and length the ranges were slightly larger and slightly smaller, respectively. Compared to the Russian group, the ranges in yield and width were twice as large, but the ranges for weight and length were only slightly larger.

For yield the low extreme overlapped the Japanese but not the Russian extreme, whereas the high extreme surpassed both groups. For weight and length, the low extremes exceeded those of both parent groups though the high extremes did not surpass those of the Japanese group, topping the Russian extreme for weight and being equal to it for length. For width, the low extreme overlapped that of the Japanese group but was equal to that of the Russian group, and the high extreme surpassed the Russian but not the Japanese extreme. For yield, there was only one high and one low transgressive segregant, and the low-parent types were dwarfed by the high-parent types, leaving nearly half as intermediates (**Figure 5.5**; **Appendix C.5**). For weight and width, there were a couple of high transgressive segregants and no low transgressive segregants as well as more high-parent types than low with a clear majority of intermediates. For length, there were similar quantities of high and low transgressive segregants as well as high- and low-parent types with a minority of intermediates.

Range in fruit length:width was from 1.29-2.21, length:weight from 11.5-30.9 mm/g and width:weight from 7.1-15.7 mm/g (**Table 5.4**). The distributions for each ratio were intermediate to those of the Japanese and Russian groups, but there was some skew toward the former for

length:width and width:weight. Compared to the Japanese group, the absolute ranges for length:width and width:weight were between half again and twice as large, but the range was four times broader for length:weight. The range for length:width was about the same as for the Russian group and only slightly larger for length:weight and width:weight.

The low extreme for length:width overlapped the low extremes of both parent groups, whereas the high extreme overlapped those of the Japanese but not the Russian group. For length:weight and width:weight, the low extremes exceeded those of the Russian but not the Japanese group and the opposite for the high extremes. For length:width, there were nearly equal proportions of low and high transgressive segregants, but there were far more low- than high-parent types with less than half as intermediates. For length:weight and width:weight, there were few transgressive segregants if any, but there were more low- than high- parent types and half were intermediates.

The Japanese/Russian group showed a high proportion of additive gene action for fruit weight and width with a low degree of transgressive segregation but skew toward dominance and overdominance of heavier and wider Japanese fruit; a moderate proportion of additive gene action for yield with a low degree of transgressive segregation that was slightly skewed toward dominance, but not overdominance, of higher Japanese yields; a low degree of additive gene action for length with extensive influence of both dominance and overdominance and a spread of observations from low to high transgressive segregation contributed from either parent; a moderate degree of additive gene action with dominance of low Russian length:width and noteworthy overdominance in both directions; and a predominance of additive gene action for length:weight and width:weight with substantial dominance of low Japanese ratios.

5.2.2.5 Improved Kuril/Russian Germplasm

The Kuril/Russian group ranged in yield from 29.4-1,706.3 g/plant, weight from 0.55-1.70 g/fruit, length from 15.1-27.1 mm and width from 9.0-14.2 mm (**Table 5.3**). The distribution for yield bore similarities to the irregular distributions of the Kuril and Russian groups, and the distributions for weight, length and width were intermediate between those of the two parent groups. Comparing against the Kuril group, the absolute ranges in yield and length were five and three times larger, respectively, and the ranges in weight and width were twice as great. Contrasted

131

with the Russian group, the ranges for yield and length were two thirds and a fifth as great, while the ranges for weight and width were twice as great and two thirds greater, respectively.

For yield, weight and length, the low and high extremes overlapped those of both parent groups, but the low extreme did not quite exceed that of the Russian group for width. For yield, there was a slightly higher proportion of low transgressive segregants than high but slightly more high- than low-parent types with half as intermediates (**Figure 5.5**; **Appendix C.5**). In contrast, for weight, length and width, there were many more high transgressive segregants and high-parent types than low, leaving a minority as intermediates.

Range in fruit length:width was from 1.47-2.74, length:weight from 15.0-33.6 mm/g and width:weight from 8.5-17.0 mm/g (**Table 5.4**). For all three ratios, the distributions were intermediate between the Russian and Kuril groups. The absolute range in length:width was many times broader than for the Kuril group and it was four and three times broader for length:weight and width:weight, respectively. Compared to the Russian group, the ranges for length:width and length:weight were three times and only slightly larger, respectively, but the range for width:weight was slightly more constrained.

The low and high extremes for length:width overlapped those of both parent groups and length:weight and width:weight overlapped all but the high extreme for the Russian group. For length:width, there were fewer low than high transgressive segregants and parent types and for width:weight there were fewer high than low transgressive segregants and parent types with less than half as intermediates. For length:weight, there were equal proportions of low and high transgressive segregants and similar proportions of low- and high-parent types, with over half as intermediates.

The Kuril/Russian group showed a moderate degree of additive gene action for yield and a high degree of transgressive segregation with little skew toward either high or low yields; a low proportion of additive gene action for weight, length and width with abundant transgressive segregation and skew toward dominance and overdominance of larger, longer Kuril and wider Russian fruit; extensive additive gene action for length:width with overdominance and some dominance of higher Russian ratios; a considerable additive gene action for length:weight with dominance of both higher and lower ratios but no skew in either direction; and lower levels of additive gene action for width:weight with skew toward dominance and overdominance of lower Kuril ratios.

5.2.2.6 Mode of Gene Action across Improved Germplasm Groups

In general, the Japanese group had high yields of large, long, wide fruit (**Section 5.2.1.2**). The Kuril group had moderate yields of moderately heavy and wide but short fruit. The Russian group had low yields of light and narrow but long fruit (**Figure 5.5**; **Appendix C.5**). Consequently, the Japanese group had moderate length:width, while the Kuril and Russian groups had low and high ratios, respectively. In contrast, the Japanese group had low length:weight and width:weight, and the Kuril and Russian groups had moderate and high ratios, respectively. Therefore, the Japanese/Russian group was the most dissortive for yield, weight, width, length:weight and width:weight, but the Japanese/Kuril and Kuril/Russian groups were more dissortive for length, the latter being most dissortive for length:width. Depending on the foundation groups used to make each improved group, these morphological measures combined in different ways.

The proportion of intermediates was high for yield, moderate for width and much lower for weight, length and all three ratios for the Japanese/Kuril group; high for weight, width and length:weight, moderate for yield, length:width and width:weight and low for length for the Japanese/Russian group; and moderate for yield, length:width and length:weight and low for weight, length, width and width:weight for the Kuril/Russian group. Across the improved germplasm, the proportion of intermediates was highest for yield, weight and length:weight, slightly lower for width, length:width and width:weight and much lower for length.

Total transgressive segregation was highest for length:width, followed closely by weight, length and width:weight but was substantially lower for yield and length:weight and nearly non-existent for width for the Japanese/Kuril group; high for length and length:width but notably lower for all other variables for the Japanese/Russian group; and high for weight, length, width and width:weight and more moderate for yield, length:width and length:width for the Kuril/Russian group. Averaged across the improved germplasm, total incidence of transgressive segregation was highest for length and length:width, followed by weight, width and width:weight, and it was very low for yield and length:weight.

Overall, there were more high- than low-parent types for all four morphological measures, but the opposite was true of the three calculated ratios. High transgressive segregation was more prevalent than low for weight, length, width and width:weight, similar for yield and the opposite for length:width and length:weight. Therefore, though additive gene action ranged from moderate

to high for yield, there was no over-arching trend in overdominance, and dominance was only seen for higher Japanese yields in the assortive Japanese/Russian group. Though additive gene action ranged from low to moderate for length, there dominance of shorter Kuril fruit in the dissortive Japanese/Kuril group contrasted with dominance of longer Russian fruit in the dissortive Kuril/Russian group, while there was a lack of skew in the assortive Japanese/Russian group. For weight and width, additive gene action was low and transgressive segregation was high for the assortive Japanese/Kuril and Kuril/Russian groups, whereas additive gene action was was high and transgressive segregation low for the dissortive Japanese/Russian group. Invariably there was skew toward dominance and overdominance of heavy, wide fruit, no matter the genetic source.

Additionally, although additive gene action ranged from low to moderate for length:width, there was a general skew in the assortive Japanese/Kuril and Japanese/Russian groups toward dominance of the lower Kuril and Japanese ratios, respectively, whereas in the assortive Kuril/Russian group there was overdominance of the higher Russian ratios. For length:weight, additive gene action was rare for the assortive Japanese/Kuril group but very high for the dissortive Japanese/Russian and assortive Kuril/Russian groups. There were low degrees of transgressive segregation but some skew toward dominance and overdominance of lower Japanese ratios for the Japanese/Kuril and Japanese/Russian groups and no skew for the Kuril/Russian group. For width:weight, additive gene action was low for the assortive Japanese/Kuril and Kuril/Russian groups that had moderate degrees of transgressive segregation with dominance and overdominance of low Japanese and Kuril ratios, respectively. The dissortive Japanese/Russian group had lower transgressive segregation and skew in dominance toward low Japanese ratios.

5.2.2.7 Correlations between Fruit Morphological Traits

At a single trial site with less biological replication than above (**Section 5.2.1.6**), there were no significant phenotypic correlations for fruit yield, but numerous correlations between other traits (**Table 5.6**). In contrast, there was a low positive correlation for fruit yield and length between hybrid/parent comparisons (i.e., correlations between statistical classifications of hybrid genotypes) in the Kuril/Russian group (**Table 5.7**). There was a positive correlation between weight and length. This correlation was high for the Kuril and Russian groups and low for the Japanese group, being intermediate between each combination of parent groups for the improved

Table 5.6. Foundation and Improved Germplasm: Pearson's correlations between fruit morphological traits for blue honeysuckle in 2012/2013 in Chilliwack, BC, Canada (only statistically significant correlations [$p < 0.05$] are shown).

		Group	r			Group	r
Weight	Length	All Germplasm	0.632	Length	Width	All Germplasm	0.415
		Japanese	0.372			Kuril	0.721
		Kuril	0.852			Russian	0.790
		Russian	0.832			Japanese/Russian	0.418
		Japanese/Kuril	0.639			Kuril/Russian	0.533
		Japanese/Russian	0.588		Length:Width	All Germplasm	0.702
		Kuril/Russian	0.708			Japanese	0.880
	Width	All Germplasm	0.810			Kuril	0.825
		Japanese	0.670			Japanese/Kuril	0.850
		Kuril	0.875			Japanese/Russian	0.708
		Russian	0.944			Kuril/Russian	0.615
		Japanese/Kuril	0.718		Length:Weight	Japanese	0.465
		Japanese/Russian	0.805			Kuril	*-0.601*
		Kuril/Russian	0.822			Russian	*-0.491*
	Length:Width	Kuril	0.470			Kuril/Russian	*-0.364*
		Russian	*-0.438*		Width:Weight	All Germplasm	*-0.627*
	Length:Weight	All Germplasm	*-0.777*			Japanese	*-0.559*
		Japanese	*-0.623*			Kuril	*-0.859*
		Kuril	*-0.865*			Russian	*-0.627*
		Russian	*-0.811*			Japanese/Kuril	*-0.627*
		Japanese/Kuril	*-0.659*			Japanese/Russian	*-0.616*
		Japanese/Russian	*-0.834*			Kuril/Russian	*-0.690*
		Kuril/Russian	*-0.832*	Width	Length:Width	All Germplasm	*-0.345*
	Width:Weight	All Germplasm	*-0.875*			Japanese	*-0.549*
		Japanese	*-0.818*			Russian	*-0.574*
		Kuril	*-0.913*			Japanese/Russian	*-0.334*
		Russian	*-0.846*			Kuril/Russian	*-0.327*
		Japanese/Kuril	*-0.902*				
		Japanese/Russian	*-0.895*				
		Kuril/Russian	*-0.875*				

Table 5.6. Continued. Foundation and Improved Germplasm: Pearson's correlations between fruit morphological traits associated with agronomic potential for blue honeysuckle in 2012/2013 in Chilliwack, BC, Canada (only statistically significant correlations [p < 0.05] are shown).

		Group	r			Group	r
Width	Length: Weight	All Germplasm	-0.765	Length: Width	Length: Weight	All Germplasm	0.435
		Japanese	-0.677			Japanese	0.715
		Kuril	-0.880			Russian	0.718
		Russian	-0.820			Japanese/Kuril	0.499
		Japanese/Kuril	-0.703			Japanese/Russian	0.410
		Japanese/Russian	-0.745			Kuril/Russian	0.326
		Kuril/Russian	-0.773		Width: Weight	Japanese	-0.388
	Width: Weight	All Germplasm	-0.627			Kuril	-0.574
		Kuril	-0.820			Russian	0.512
		Russian	-0.810			Japanese/Kuril	-0.326
		Japanese/Kuril	-0.527	Length: Weight	Width: Weight	All Germplasm	0.808
		Japanese/Russian	-0.584			Japanese	0.365
		Kuril/Russian	-0.633			Kuril	0.890
						Russian	0.961
						Japanese/Kuril	0.634
						Japanese/Russian	0.801
						Kuril/Russian	0.857

Table 5.7. Improved Germplasm: Rho correlations between statistical classifications of improved hybrid blue honeysuckle genotypes for fruit morphological traits in 2012/2013 in Chilliwack, BC, Canada (p < 0.05).

		Group	r
Yield	Length	Kuril/Russian	0.312
Weight	Length	All Improved	0.399
		Japanese/Kuril	0.763
		Kuril/Russian	0.460
	Width	All Improved	0.746
		Japanese/Kuril	0.440
		Japanese/Russian	0.802
		Kuril/Russian	0.796
	Length:Width	Japanese/Kuril	0.506
	Length:Weight	All Improved	*-0.634*
		Japanese/Kuril	*-0.563*
		Japanese/Russian	*-0.629*
		Kuril/Russian	*-0.743*
	Width:Weight	All Improved	*-0.803*
		Japanese/Kuril	*-0.893*
		Japanese/Russian	*-0.653*
		Kuril/Russian	*-0.840*
Length	Length:Width	All Improved	0.683
		Japanese/Kuril	0.804
		Japanese/Russian	0.639
		Kuril/Russian	0.709

		Group	r
Length	Width:Weight	All Improved	*-0.501*
		Japanese/Kuril	*-0.878*
		Kuril/Russian	*-0.543*
	Length:Width	Japanese/Russian	*-0.370*
Width	Length:Weight	All Improved	*-0.662*
		Japanese/Kuril	*-0.605*
		Japanese/Russian	*-0.659*
		Kuril/Russian	*-0.738*
	Width:Weight	All Improved	*-0.470*
		Japanese/Russian	*-0.378*
		Kuril/Russian	*-0.582*
Length: Width	Length:Weight	All Improved	0.362
		Japanese/Russian	0.668
	Width:Weight	Japanese/Kuril	*-0.745*
Length: Weight	Width:Weight	All Improved	0.485
		Japanese/Kuril	0.343
		Japanese/Russian	0.372
		Kuril/Russian	0.637

groups. Hybrid/parent comparisons demonstrated a low positive correlation across the improved germplasm, which was high and low in the Japanese/Kuril and Kuril/Russian groups on their own, respectively. There were high phenotypic correlations between weight and width in the three improved groups, relative strengths of correlation reflecting moderate, high and very high correlations in the Japanese, Kuril and Russian groups, respectively. In corroboration, hybrid/parent comparisons showed a high positive correlation in skew across the improved germplasm that was high in the Japanese/Russian and Kuril/Russian groups and low in the Japanese/Kuril group on their own. For length and width, there were only low and moderate positive associations in the Japanese/Russian and Kuril/Russian groups, respectively, and no correlation across the improved germplasm.

The improved group with the highest correlation between weight and length was the combination of foundation germplasm with the highest correlations. For hybrid/parent comparisons, differences in the strength of correlation between improved germplasm did not reflect the differences in phenotypic correlations across combinations of foundation groups. When the Japanese and Kuril groups combined, there was a high correlation between the dominance and overdominance of heavier and longer fruit. When the Kuril and Russian groups combined, there was a lower correlation between the dominance and overdominance of heavier and longer fruit. When the Japanese and Russian groups combined, there was no significant correlation between the dominance and overdominance of heavier and longer fruit because there was virtually no skew for the latter.

For weight and width, the higher the correlations between the two parental groups, the higher the correlation in the resulting improved group. When the Russian group combined with either the Japanese or Kuril group, there was a high degree of association between the dominance and overdominance of heavier and broader fruit. When the Japanese and Kuril groups combined, there was a low correlation between dominance and overdominance in heavier and broader fruit. Fruit weight had moderate to high correlations with length:weight and high to very high correlations with width:weight. The Japanese/Kuril group had the lowest correlation for length:weight and the highest correlation for width:weight, while the Japanese/Russian and Kuril/Russian groups had similar correlations for both.

There was a moderate to high negative correlation between length and width:weight in consequence of their common correlations with width and weight. This moderate negative

correlation across all groups was as strong, or stronger, in each group on its own. Also, there were high and moderate negative correlation between hybrid/parent comparisons in the Japanese/Kuril and Kuril/Russian groups, respectively, which reflects the strengths of phenotypic correlation in their respective parent groups and the fact that fruit length was skewed toward high transgressive segregants and high-parent types for these two improved groups and not the Japanese/Russian group.

Equally, there was a negative relationship between width and length:weight seen through correlations in phenotypic values and hybrid/parent comparisons. Phenotypically, there was a high negative correlation between these two variables in most foundation and improved groups on their own, only the correlation for the Japanese group being moderate in strength. The correlation in hybrid/parent comparisons was moderate across the improved germplasm and for the Japanese/Kuril and Japanese/Russian groups on their own but high for the Kuril/Russian group, reflecting a higher phenotypic correlation for this group.

5.2.3   Fruit Shapes of Foundation Germplasm
5.2.3.1 Japanese Foundation Germplasm

Japanese fruit shapes were highly variable, with nine different unique combinations of 1° and 2° shapes in eleven genotypes (**Figure 5.6**; **Table 5.8**). More than a third of genotypes had ovate 1° shapes and approximately a quarter had oblong, cylindrical and bottle shapes, while torpedo shapes were slightly less common. A quarter of genotypes had oblong and cylindrical 2° shapes, but bottle, ovate and spindle shapes were less widespread. Overall, more than half of genotypes had oblong and cylindrical shapes and just under half had ovate shapes, while torpedo and spindle shapes were relatively rare. Almost half the time, oblong and ovate shapes were found together as well as cylindrical with bottle shapes (**Table 5.9**). Other common associations were oblong with cylindrical, oblong with bottle and ovate with cylindrical. All other combinations of shapes were infrequent. Proximal end shapes were truncated for three genotypes, truncated or rounded for five genotypes and primarily truncated and secondarily rounded for three genotypes. Most genotypes had rounded 1° distal end shapes, but more than half also had indented and some had peaked or flat ends. Almost half had flat 2° distal end shapes, but two genotypes also had rounded or indented shapes.

Shimoyama (2008) reports primarily oval, ovate and bottle shapes in Japanese germplasm
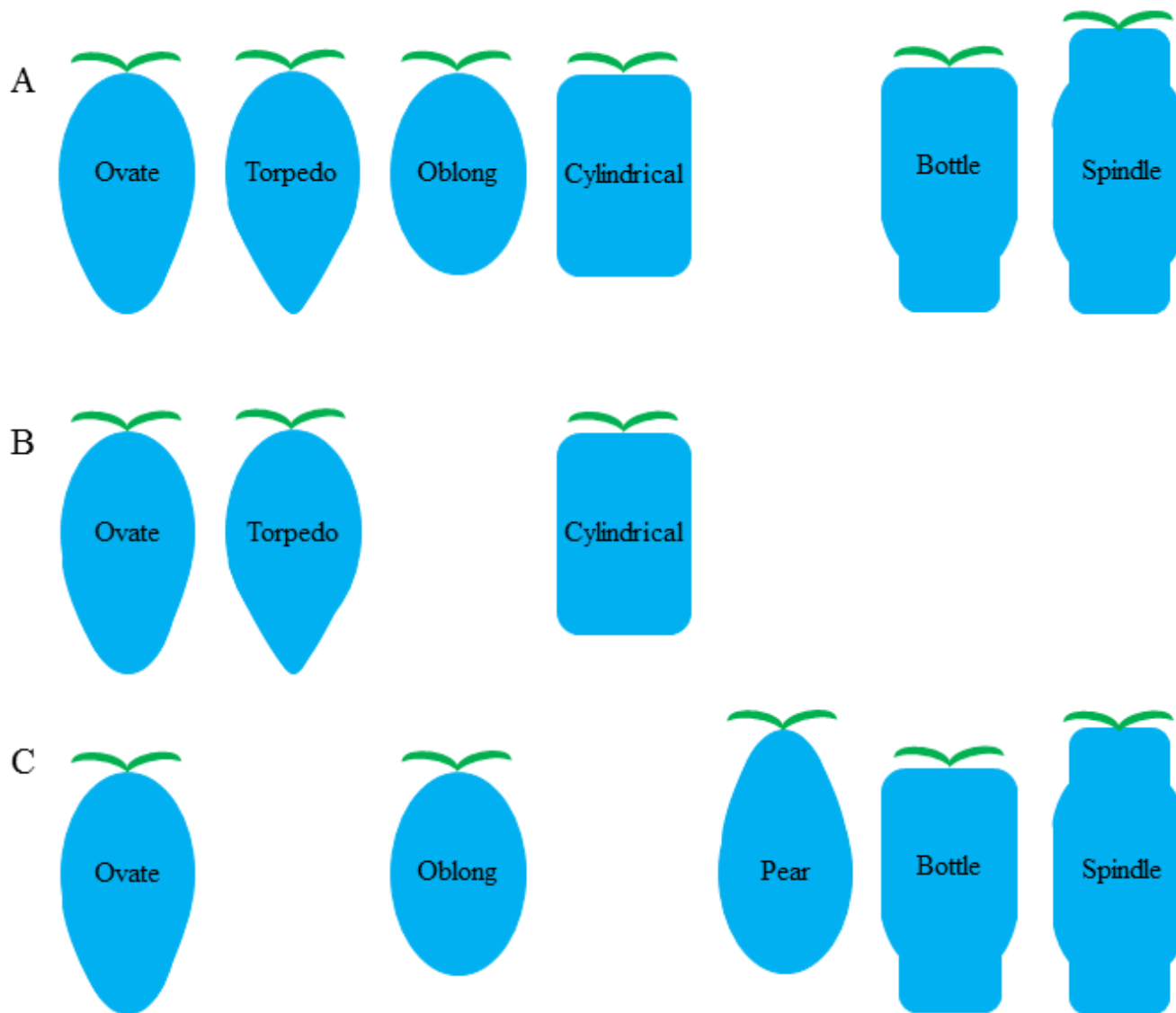
Figure 5.6. Foundation Germplasm: Fruit shapes observed in blue honeysuckle in 2012/2013 in the Fraser Valley, BC, Canada (A) Japanese group (B) Kuril group (C) Russian group.

Table 5.8. Foundation Germplasm: Unique combinations of 1° and 2° fruit shapes and proximal and distal end shapes in blue honeysuckle in 2012/2013 in the Fraser Valley, BC, Canada (J – Japanese, K – Kuril, R – Russian).

Genotype	Fruit Shape(s)	Proximal End Shape(s)	Distal End Shape(s)
J-21-78	Primarily bottle & some cylinders	Truncate	Indented
J-22-14	Primarily torpedo & some cylindrical & bottle	Truncate	Primarily peaked & some flat & indented
J-41-83	Primarily ovate & torpedo & some oblong	Primarily truncate & some round	Round & peaked
J-42-45	Primarily ovate & some cylindrical & oblong	Primarily truncate & some round	Primarily round & some flat & indented
J-43-87	Primarily ovate & cylindrical & some oblong	Round & truncate	Primarily round & some flat
J-444-39	Primarily cylindrical & oblong & some bottle	Round & truncate	Round & indented
J-45-14	Primarily cylindrical & oblong & some bottle	Round & truncate	Primarily round & indented & some flat
J-46-55	Primarily oblong & bottle & some spindle	Round & truncate	Round & indented
J-56-18	Primarily cylindrical & bottle & some ovate	Truncate	Primarily flat & indented & some round
J-66-53	Primarily ovate & torpedo & some oblong	Primarily truncate & some round	Primarily round & peaked & some flat
J-73-39	Ovate & oblong	Round & truncate	Round & indented
K-3-03	Primarily oblong & cylindrical & some ovate	Round & truncate	Round & indented
K-3-05	Primarily oblong & cylindrical & some ovate	Round & truncate	Round & indented
K-3-06	Primarily oblong & cylindrical & some ovate	Round & truncate	Round & indented
K-3-07	Primarily oblong & cylindrical & some ovate	Round & truncate	Round & indented
K-97-12	Primarily ovate & cylindrical & some oblong	Round & truncate	Flat & round

Table 5.8. Continued. Foundation Germplasm: Unique combinations of 1° and 2° fruit shapes and proximal and distal end shapes in blue honeysuckle in 2012/2013 in the Fraser Valley, BC, Canada (J – Japanese, K – Kuril, R – Russian).

Genotype	Fruit Shape(s)	Proximal End Shape(s)	Distal End Shape(s)
R-2-06	Primarily spindle & some bottle	Acute & round	Indented
R-2-07	Primarily ovate & oblong & some spindle	Acute & round	Primarily round & peaked & some indented
R-2-10	Primarily bottle & some oblong	Round & truncate	Primarily indented & some round
R-2-11	Primarily oblong & some pear	Round	Round
R-2-13	Oblong	Round	Round
R-2-14	Primarily oblong & some bottle	Acute & round	Primarily round & peaked & some indented
R-2-16	Primarily bell & some bottle	Acute & round	Indented
R-27-35	Oblong	Acute & round	Round & peaked
J-PP	Primarily oblong & some bottle & torpedo	Round	Primarily round & some indented & peaked
'Borealis'	Primarily oblong & pear & some ovate	Round	Round
'Tundra'	Primarily oblong & cylindrical & some pear	Round & truncate	Flat, round & indented
'Indigo Gem'	Primarily oblong & cylindrical & some bottle	Round & truncate	Flat, round & indented

Table 5.9. Foundation Germplasm: Proportion of genotypes in which each combination of fruit shapes was associated in blue honeysuckle in 2012/2013 in the Fraser Valley, BC, Canada.

Japanese (11 Genotypes)

	Ovate	Torpedo	Oblong	Cylindrical	Bell	Pear	Bottle	Spindle
Torpedo	9.1%							
Oblong	45.5%	9.1%						
Cylindrical	27.3%	9.1%	36.4%					
Bell								
Pear								
Bottle	9.1%	9.1%	27.3%	45.5%				
Spindle			9.1%			9.1%		
Pod								

Kuril (5 Genotypes)

	Ovate	Torpedo	Oblong	Cylindrical	Bell	Pear	Bottle	Spindle
Torpedo								
Oblong	100.0%							
Cylindrical	100.0%		100.0%					
Bell								
Pear								
Bottle								
Spindle								
Pod								

Russian (8 Genotypes)

	Ovate	Torpedo	Oblong	Cylindrical	Bell	Pear	Bottle	Spindle
Torpedo								
Oblong	12.5%							
Cylindrical								
Bell								
Pear			12.5%					
Bottle			25.0%		12.5%			
Spindle	12.5%		12.5%			12.5%		
Pod								

but also round, cylindrical and pear. Accordingly, oval, ovate and bottle shapes were widespread in the current study. In contrast, cylindrical shapes were also common and there were more torpedo and spindle than round or pear shapes. Thompson (2006b) records oblong and football (i.e., short and long oblong), cylindrical, jug (i.e., bottle), pear and round shapes, suggesting that Japanese fruit are typically broader than Russian. Most of these shapes were observed in the current study, whereas a greater average width for the Japanese germplasm (**Section 5.2.1.1**) corroborates the statement about breadth. From analysis of the proximal and distal end shapes, there is little to suggest that Japanese fruit are rounder, as proposed by Bors (2009), but rather that they have a lower fruit length:width than the Russian group, the Kuril group having a lower ratio still (**Section 5.2.1.1**). At the U of S, J-22-14 is described as cylindrical and heart-shaped (i.e., torpedo), J-41-83 as bullet-shaped (i.e., torpedo) and J-73-39 as oval, which are confirmed in the current study, but J-42-45 is, contradictorily, described as round and J-73-39 as oval (Bors et al 2012), which was only a 2° shape in the current study. Apparently, variability in fruit shape manifests differently across environments and based on the system of classification in use.

5.2.3.2 Kuril Foundation Germplasm

All four late (**Section 4.2.1.1**) Kuril cultivars had the same overall fruit shape: 1° oblong and cylindrical with 2° ovate shapes (**Table 5.8**). K-97-12 had the same fruit shapes, but ovate and cylindrical were 1° with only oblong as 2° shapes. Therefore, all Kuril genotypes had cylindrical as a 1° shape with one outlier genotype having a greater proportion of ovate than oblong in contrast with the other genotypes. Oblong, ovate and cylindrical shapes were associated in the Kuril group. However, torpedo, bell, pear, bottle, spindle and pod shapes were not found at all (**Table 5.9**). All genotypes had a mixture of two 1° shapes with an accompanying 2° fruit shape, but these shapes were all very similar because of low variability in Kuril fruit shapes (**Section 5.2.1.4**). Rounded and truncated 1° proximal end shapes were seen for all five genotypes. Rounded distal end shapes were seen for all five Kuril genotypes, while four had indented and one had flat (K-97-12) 1° shapes as well. There were no 2° proximal or distal end shapes.

Based on plant exploration in the Kuril Islands (Sabitov et al 2007), Kuril fruit shapes in the wild resemble torpedoes, but evaluations in Corvallis (Thompson and Chaovanalikit 2003) and Saskatchewan (Bors et al 2009) suggest predominance of oval shapes. The current study concurs more closely with these latter two reports, though a mixture of more abrupt end shapes often

resulted in cylindrical shapes as well. It should be noted that the Kuril material included in breeding populations is descendant from a single clone from Iterup island, which may skew these observations of current crop genetic resources. Also, ovate shapes were observed, rather than torpedo, resulting from distal end shapes that were more rounded than acute in asymmetrically shaped fruit. Relatively round shapes, compared to the Japanese and Russian germplasm, are also reported from Saskatchewan (Bors 2009), which is confirmed by the Kuril group's low fruit length:width (**Section 5.2.1.3**).

5.2.3.3 Russian Foundation Germplasm

There was a different combination of fruit shapes for each Russian genotype except for R-2-13 and R-27-35, which shared oblong as their sole fruit shape (**Table 5.8**). A single $1°$ shape (bell, bottle, oblong or spindle) was attributed for each genotype except for R-2-07, which had both ovate and oblong $1°$ shapes. Therefore, fruit shape was highly variable between Russian genotypes, but highly consistent within genotypes. The $1°$ shapes were bell, bottle, oblong, ovate and spindle, with pear shapes only included as $2°$ shapes. Ovate, oblong and spindle shapes were associated in one genotype, whereas oblong shapes were associated with pear and bottle in one and two genotypes, respectively (**Table 5.9**). Associations of bell with bottle and bottle with spindle shapes were seen in a single genotype each. Oblong shapes were most ubiquitous, being $1°$ in half the Russian group and $2°$ in one more. Bottle shapes were only $1°$ in a single genotype but $2°$ in three others. Spindle shapes were $1°$ in one and $2°$ in another, while pear was only $2°$ in a single genotype. Ovate and bell shapes were $1°$ in only one genotype each, and the former was combined with oblong $1°$ shapes. Proximal end shapes were rounded for eight, acute for five and truncate in just one genotype without any $2°$ shapes. Distal end shapes were rounded for five, indented and peaked for three genotypes each, but only a few rounded and indented $2°$ shape were observed.

These shape categorizations were conducted by adaptation of the original Russian germplasm descriptor (Plekhanova 1988), which included round, oblong, cylindrical, ovate, torpedo (i.e., obovate), pear, bottle, bell, spindle and pod shapes. Except for round and pod, each of these shapes was found in the Russian group in the current study. Round shapes do not exist in the Russian germplasm collection at the U of S, but they are found in Russia breeding programs (Bors 2009). Pod shapes may be merely abnormalities in fruit development (**Section 5.2.4.8**).

5.2.3.4 Comparison of Foundation Germplasm Groups

The most universal $1°$ fruit shape in the foundation germplasm was oblong (45.8%), followed by cylindrical (33.3%), ovate (25.0%) and bottle (17.0%). Torpedo (8.3%), bell (4.2%) and spindle (4.2%) shapes were less common, and pear shapes were not observed as a $1°$ shape. Oblong, ovate and bottle shapes were equally pervasive as $2°$ shapes (20.8% each) with some cylindrical (12.5%), spindle (8.3%) and pear (4.2%) $2°$ shapes as well. Overall, oblong shapes were found in two thirds of the foundation genotypes and cylindrical and ovate in 45.8% each, followed in descending order by bottle (37.5%), spindle (12.5%), torpedo (8.3%) and bell and pear (4.2% each) shapes.

The Japanese and Kuril groups shared oblong, ovate and cylindrical shapes, but the Japanese group also had torpedo and bottle shapes. The three shapes held in common were associated with one another in both foundation groups. For the Japanese group, torpedo and bottle shapes were associated with each common shape, but bottles were more often seen with oblong and cylindrical than with ovate shapes. Overall, a broader range of shape combinations was seen for the Japanese than the Kuril group.

The Japanese and Russian groups shared ovate, oblong, bottle and spindle shapes, but differed in that the Japanese had torpedo and cylindrical compared to the Russian group's bell and ovate shapes. Oblong and bottle shapes were principal in both foundation groups, whereas ovate shapes were common in only the Japanese group. Cylindrical was prevalent in the Japanese group and not found in the Russian group at all, and spindles were detected occasionally in each group. The Japanese and Russian groups shared diversity (i.e., six overall shapes), but it manifested differently, the former demonstrating greater within-genotype diversity (i.e., combinations of shapes) and the latter having greater between-genotype diversity (i.e., greater distinctions in shapes across the group). This resulted in fewer associations between shapes for the Russian group than the Japanese group, which is not surprising given the relatively narrower range in geographic origin for the latter group.

The Kuril group was more homogenous than the Russian and Japanese groups. The two groups shared oblong and ovate shapes, the Russian group not having the cylindrical shapes seen in the Kuril group. The only shape association held in common, between ovate and oblong, was found in all the Kuril genotypes but only R-2-07 in the Russian group. However, the Russian group had bell, pear, bottle and spindle shapes not found for the Kuril group.

The Japanese were unique for torpedo shapes and the Russian group for bell and pear shapes. The Kuril group, having only the three principal shapes, had no unique shapes of its own. The Japanese and Kuril groups shared cylindrical shapes not found in the Russian group, whereas the Japanese and Russian groups shared bottle and spindle shapes not found in the Kuril group. The Kuril and Russian groups were the most disparate in diversity and commonality of shapes, but the Japanese group shared the same common shapes with the Kuril group and shared diversity of shapes with the Russian group. The Japanese and Kuril groups also shared within-genotype diversity, and the Russian group's diversity was primarily between-genotypes. Overall, there were few Kuril fruit shapes, but there were combinations of shapes within each genotype. There were many Japanese shapes and there were combinations of shapes within most genotypes. There were many shapes for the Russian group, but combinations of shapes were rarer for each genotype. In other words, within-genotype diversity was low for the Russian group and high in the Kuril and Japanese groups, and between-genotype diversity was low in the Kuril group and high in the Japanese and Russian groups.

5.2.3.5 Out-group Comparison Genotypes

Each out-group comparison genotype had a distinct fruit shape combination (**Table 5.8**). J-PP had oblong $1°$ shapes and $2°$ bottle and torpedo shapes. This compared similarly with the Japanese foundation group for which oblong, bottle and torpedo shapes were both pervasive and associated. 'Borealis' and 'Tundra' had oblong and cylindrical $1°$ shapes, the former having $2°$ bottle and the latter $2°$ pear shapes. 'Indigo Gem' had oblong and pear $1°$ shapes and $2°$ ovate shapes. The three U of S cultivars shared oblong $1°$ shapes, but 'Indigo Gem' differed from 'Borealis' and 'Tundra' in having additional pear rather than cylindrical $1°$ shapes. The three cultivars differed in $2°$ shapes, from bottle ('Borealis') to pear ('Tundra') to ovate ('Indigo Gem'). In comparison, the female parent (K-97-12) had ovate and cylindrical $1°$ shapes and oblong $2°$ shape (**Section 5.2.3.2**), but no literature source lists the shape for the male parent (Berry Belle™).

'Borealis' is described as a "short flat box", 'Tundra' as a "flat bullet oval" and 'Indigo Gem' as a "robust short oval" at the U of S (Bors 2009). These descriptions bear similarities to the current study: the relative shortness of 'Indigo Gem' is evidenced by the lowest fruit length:width (**Section 5.2.1.5**); and the rounder shapes of 'Borealis' and 'Tundra' are noted for their potential to roll on a sorting belt, contributing improved machine harvestability over Russian

147

germplasm (Bors et al 2009). Very tight and tight fruit attachment (**Section 5.2.5.7**) for 'Borealis' and 'Tundra' contradict these suggestions of suitability for machine harvest.

5.2.3.6 An Anatomical Explanation of Fruit Shape in Blue Honeysuckle

Fruit shapes are not only highly variable between blue honeysuckle genotypes, but vary dramatically within genotypes and even within harvests of fruit from an individual plant. The fruit of a single plant can manifest one to four distinguishable fruit shapes at the same time, presumably depending on many different environmental factors affecting fruit development. With the same genetic program, one fruit may be oblong with rounded proximal and distal end shapes, whereas a fruit two nodes down on the same stem there will be bell-shaped fruit with an indented distal end, cylindrical-shaped fruit with a truncated proximal end and a flat or indented distal end or even ovate-shaped fruit with relative tapering to the distal end. This variation is related to blue honeysuckle's unique fruit anatomy as a multiple fruit formed by synanthy of accessory tissues.

Blue honeysuckle fruit are a pseudocarp, specifically a "false berry" formed by "false synanthy" with four bractlets making a cupula (i.e., inverted cup or dome). Synanthy is defined as the "union of two or more members of an inflorescence" and, though widespread across plant species, it is not common (Arber 1903). The type of synanthy observed in blue honeysuckle is the only example of its kind in the Caprifoliaceae, being a "false" form of synanthy resulting from enclosure by non-floral tissue rather than amalgamation of the receptacle walls of the two ovaries (Arber 1903). The central two prophylls of each of the two lateral flowers of this two-flowered cyme (i.e., dichasium with suppressed terminal flower) are the non-floral bract tissues that form the fleshy sheath around the fruit (Rehder 1909).

The immense phenotypic variation in overall fruit shape is connected to diversity in smaller component characters: fruit shape in cross-section, distal fruit opening size (**Section 5.2.5.3**), proximal and distal end shapes, overall length and width (**Section 5.2.1**) and the relative distribution of fruit tissues within the accessory layer that varies in length. Genetic factors, in turn, interact with environmental factors (e.g., weather, temperature, moisture, nutritional and crop load) that influence pollination and fruit set and development. Of importance is the effect of pollination as the degree of pollination on fruit size and shape is a relevant to the amount of within-genotype variation observed in blue honeysuckle. For example, though each ovary contains eleven ovules for a potential 22 seeds per fruit (Thompson 2006a), anything above seven or eight seeds per fruit

is often sufficient for adequate fruit sizing (M. Thompson, pers. comm. 2010-06-15). Therefore, in the Fraser Valley, poor pollination of Russian blue honeysuckle is associated with a bloom period that is far too early for normal activity of pollinating insects (**Section 4.2.1.2**), resulting in poor fruit formation and low productivity (**Section 5.2.1.4**).

Blue honeysuckle is also prone to developmental abnormalities that result in within-genotype shape variation, principally incomplete synanthy of the fruit capsule. This may be caused by release of third terminal flower from its usual suppression (i.e., triple flowering) (Ashimov et al 2009), but duplicated floral organs and uneven or incomplete growth of the accessory layer surrounding the fruit are very common (**Section 5.2.5.1**).

While these environmentally-regulated phenomena undoubtedly have a genetic basis, more routine variation in shape is associated with the fact that the ovaries are completely free of each other inside the bracteolar sheath. The ovaries are connected to the inside of the sheath, resulting in its concomitant growth with the true fruit tissues, but these connections are present in some planes (i.e., the median plane at the proximal end) and not in others (i.e., the lateral plane at the proximal end and the distal end in either plane) (Arber 1903). Therefore, variability in the length of the capsule relative to the enclosed fruit, the position of the fruit within the capsule and the size and shape of the true fruit within result in a broad range of overall fruit shapes, proximal and distal end shapes and degrees to which the distal end opens and the accessory layer rolls back upon itself. Therefore, within-genotype variability can be understood as a response to variation in the factors that differentially influence fruit sizing compared to the genetic predisposition for relative growth of the fruit and accessory layer that surround them.

Further, the distal end of the fruit can be either separated from the outer accessory layer or be in close contact with it, while not actually being physically fused (**Section 5.2.4.3**). If the two tissues are in contact and the accessory layer is longer than the fruit within, a rolled edge of accessory tissue will result in an indented distal end shape. If the two tissues are in contact and the fruit within are not surpassed in length by the accessory layer, no rolled edge will form, and a flat, rounded or acute distal end shape with a small fruit opening will typically permit the distal end of the fruit to be visible to the exterior. If the two tissues do not maintain contact and the fruit within are shorter than the accessory layer, a flat, rounded or acute distal end shape with a small opening will expose an empty space on the inside of the capsule due to redaction of the fruit's distal end out of sight to the exterior. The various appearances of the distal end are, therefore,

related to the degree of contact between the accessory layer and distal fruit tissues as well as the relative lengths of these tissues to one another. Moreover, the shape and distribution of the fruit within the accessory layer complicate shapes, interacting with various combinations of proximal and distal end shapes and resulting in associations between distinct fruit shapes (**Section 5.2.4.10**).

5.2.4   Fruit Shapes of Improved Germplasm
5.2.4.1 Improved Japanese/Kuril Germplasm Fruit Shapes

The Japanese/Kuril group's $1°$ fruit shapes were cylindrical (34.4%), ovate (28.1%), oblong (25.0%) and torpedo (12.5%) (**Table 5.10**). Correspondingly, $2°$ shapes were oblong (40.6%), ovate (21.9%), bottle and cylindrical (12.5%), with occasional torpedo, pear and bell shapes. Combined, oblong was the principal shape (65.6%), followed by ovate (50.0%), cylindrical (46.9%) and torpedo (21.9%). Bottle, pear and bell shapes were present in smaller proportions.

Oblong shapes were associated with ovate and cylindrical in about a third of genotypes, and ovate shapes were associated with torpedo and cylindrical in approximately a quarter (**Table 5.11**). The $2°$ bell, pear and bottle shapes were less universal and were associated with a variety of different $1°$ shapes: most bottle and all pear shapes were $2°$ shapes to $1°$ cylindrical or oblong shapes or both, and bell shapes complemented cylindrical and oblong $1°$ shapes. Combined, cylindrical, oblong, ovate and torpedo $1°$ shapes predominated, either singly or in association. When there was more than one $1°$ shape, cylindrical was found with oblong and ovate with torpedo.

For 32 Japanese/Kuril genotypes, there were 23 unique combinations of $1°$ and $2°$ shapes, meaning the majority (59%) were a unique combination (**Appendix C.6**), but several combinations were more important: $1°$ ovate and $2°$ cylindrical and oblong shapes in five genotypes; $1°$ cylindrical and oblong and $2°$ ovate shapes in three genotypes; $1°$ cylindrical and oblong without $2°$ shapes in three genotypes; and $1°$ cylindrical and $2°$ ovate and oblong shapes in two genotypes.

5.2.4.2 Improved Japanese/Russian Germplasm Fruit Shapes

The Japanese/Russian group's most pervasive $1°$ fruit shapes were oblong and cylindrical (31.3% each) with bottle shapes in a considerable portion (15.6%), followed by ovate, pear, torpedo and bell shapes in descending order (**Table 5.10**). Oblong was also the most prevalent $2°$ shape (20.3%) with bottle, ovate, cylindrical, bell, torpedo, pear, spindle and pod shapes in lower proportions. Combined, oblong, cylindrical and bottle shapes were seen in about half (51.6%),

150

Table 5.10. Foundation and Improved Germplasm: Proportions of 1° and 2° fruit shapes in blue honeysuckle in 2012/2013 in Chilliwack, BC, Canada.

	Japanese			Kuril			Russian			All Foundation		
	1°	2°	All	1°	2°	All	1°	2°	All	1°	2°	All
Ovate	36.4%	9.1%	45.5%	20.0%	80.0%	100.0%	12.5%		12.5%	25.0%	20.8%	45.8%
Torpedo	18.2%		18.2%							8.3%		8.3%
Oblong (oval)	27.3%	27.3%	54.5%	80.0%	20.0%	100.0%	50.0%	12.5%	62.5%	45.8%	20.8%	66.7%
Cylindrical (elongate)	27.3%	27.3%	54.5%	100.0%		100.0%				33.3%	12.5%	45.8%
Bell							12.5%		12.5%	4.2%		4.2%
Pear (obovate)							0.0%	12.5%	12.5%		4.2%	4.2%
Bottle	27.3%	18.2%	45.5%				12.5%	37.5%	50.0%	16.7%	20.8%	37.5%
Spindle		9.1%	9.1%				12.5%	12.5%	25.0%	4.2%	8.3%	12.5%
Pod (banana)												

Table 5.10. Continued. Foundation and Improved Germplasm: Proportions of 1° and 2° fruit shapes in blue honeysuckle in 2012/2013 in Chilliwack, BC, Canada.

	Japanese/Kuril			Japanese/Russian			Kuril/Russian			All Improved		
	1°	2°	All	1°	2°	All	1°	2°	All	1°	2°	All
Ovate	28.1%	21.9%	50.0%	9.4%	10.9%	20.3%	3.4%	6.8%	10.2%	11.0%	11.6%	22.6%
Torpedo	12.5%	9.4%	21.9%	4.7%	6.3%	10.9%	3.4%		3.4%	5.8%	4.5%	10.3%
Oblong (oval)	25.0%	40.6%	65.6%	31.3%	20.3%	51.6%	28.8%	13.6%	42.4%	29.0%	21.9%	51.0%
Cylindrical (elongate)	34.4%	12.5%	46.9%	31.3%	9.4%	40.6%	23.7%	5.1%	28.8%	29.0%	8.4%	37.4%
Bell		3.1%	3.1%	1.6%	9.4%	10.9%	5.1%	6.8%	11.9%	2.6%	7.1%	9.7%
Pear (obovate)		9.4%	9.4%	7.8%	6.3%	14.1%	5.1%	10.2%	15.3%	5.2%	8.4%	13.5%
Bottle		12.5%	12.5%	15.6%	14.1%	29.7%	10.2%	8.5%	18.6%	10.3%	11.6%	21.9%
Spindle					1.6%	1.6%		1.7%	1.7%		1.3%	1.3%
Pod (banana)					1.6%	1.6%					0.6%	0.6%

Table 5.11. Improved Germplasm: Proportion of genotypes with each association of fruit shapes in blue honeysuckle in 2012/2013 in Chilliwack, BC, Canada.

Japanese/Kuril (32 Genotypes)

	Ovate	Torpedo	Oblong	Cylindrical	Bell	Pear	Bottle	Spindle
Torpedo	21.9%							
Oblong	34.4%	12.5%						
Cylindrical	25.0%	3.1%	31.3%					
Bell			3.1%	3.1%				
Pear	3.1%		6.3%	6.3%				
Bottle	6.3%	3.1%	3.1%	9.4%				
Spindle								
Pod								

Japanese/Russian (64 Genotypes)

	Ovate	Torpedo	Oblong	Cylindrical	Bell	Pear	Bottle	Spindle
Torpedo	3.1%							
Oblong	12.5%	9.4%						
Cylindrical	10.9%	3.1%	29.7%					
Bell	1.6%		3.1%	4.7%				
Pear			9.4%	6.3%	1.6%			
Bottle	6.3%		17.2%	15.6%	6.3%	1.6%		
Spindle						1.6%		
Pod		1.6%	1.6%					

Kuril/Russian (59 Genotypes)

	Ovate	Torpedo	Oblong	Cylindrical	Bell	Pear	Bottle	Spindle
Torpedo	3.4%							
Oblong	6.8%	3.4%						
Cylindrical	3.4%		23.7%					
Bell			8.5%	3.4%				
Pear	1.7%		13.6%	6.8%	5.1%			
Bottle	1.7%		11.9%	11.9%	1.7%			
Spindle						1.7%		
Pod								

two fifths (40.6%) and a third (29.7%) of genotypes, respectively. Ovate (20.3%), pear (14.1%) and torpedo and bell shapes (10.9% each) were less common.

The clearest shape association was between oblong and cylindrical shapes, which were observed together in approximately a third of genotypes (**Table 5.11**). Bottle shapes, either $1°$ or $2°$, were detected in regular association with bell, cylindrical and oblong shapes. Pear shapes were not rare and were associated with either cylindrical or oblong shapes or both except when they were the sole $1°$ shape as for three genotypes that had $2°$ bottle, oblong and spindle shapes, respectively. Bell shapes were almost exclusively found in association with bottle or pear shapes. Ovate shapes were $2°$ to bottle, cylindrical or oblong shapes or a combination thereof. Torpedo shapes were discovered with cylindrical, oblong or ovate shapes, while pod shapes were $2°$ to torpedo and oblong $1°$ shapes in a single genotype. Spindle and torpedo shapes were found in one and two genotypes, respectively.

For 64 Japanese/Russian genotypes, there were 46 unique combinations of $1°$ and $2°$ shapes, meaning nearly three quarters of genotypes had their own unique shape combination (**Appendix C.6**). While 12 different $1°$ and $2°$ shape combinations were scored for two genotypes each, only two combinations were seen in more: $1°$ oblong and cylindrical without $2°$ shapes in four genotypes; and $1°$ ovate and cylindrical with $2°$ oblong shapes in another four.

5.2.4.3 Improved Kuril/Russian Germplasm Fruit Shapes

For the Kuril/Russian group, the most widespread $1°$ shapes were oblong (28.8%) and cylindrical (23.7%), but smaller proportions were observed for bottle (10.2%), bell and pear (5.1% each) and ovate and torpedo (3.4% each) shapes (**Table 5.10**). Oblong shapes were also the most common $2°$ shape (13.6%), with pear, bottle, bell and ovate, cylindrical and spindle shapes following in descending order. Combined, oblong shapes were found in approximately two fifths of all Kuril/Russian genotypes (42.4%) with cylindrical shapes in more than a quarter (28.8%) and bottle, pear, bell and ovate shapes in a fifth to a tenth.

The strongest association was between oblong and cylindrical shapes, but this association was found in less than a quarter of genotypes (**Table 5.11**). Even less frequent associations were seen between bottle and oblong, bottle and cylindrical and pear and oblong shapes.

Five genotypes did not produce sufficient fruit for evaluation. Therefore, 59 of 64 Kuril/Russian genotypes presented 31 unique combinations of $1°$ and $2°$ fruit shapes (**Appendix**

C.6). Less than a third of genotypes had their own unique $1°$ and $2°$ shape combination. Ten different combinations were rated for two or three genotypes, whereas four had $1°$ cylindrical and oblong with $2°$ bottle shapes, six had $1°$ cylindrical and bottle shapes and seven had $1°$ oblong and cylindrical shapes. The most important shape for the Kuril/Russian group was cylindrical with either $2°$ bottle or oblong shapes depending on the distal end shape.

5.2.4.4 Comparison of Japanese/Kuril with Foundation Germplasm

With a few exceptions, the series of $1°$ fruit shapes in the Japanese/Kuril group was largely expected based on the parental foundation groups (**Section 5.2.3.4**). Cylindrical, oblong and ovate $1°$ shapes were found in both parental groups, whereas bottle and torpedo shapes were discovered in only the Japanese group, but $2°$ pear and bell shapes were not seen in either parental group. The widespread associations of oblong with ovate, cylindrical with ovate and cylindrical with oblong shapes that were seen in both parental foundation groups were also the three most prevalent associations in the Japanese/Kuril group. There were no other fruit shape associations in the Kuril group because of the overall limited diversity in shapes, yet some of the less important Japanese associations were also reflected in the Japanese/Kuril group. Specifically, coincidence of ovate with torpedo, oblong with torpedo and bottle with cylindrical shapes were seen in both the Japanese and Japanese/Kuril groups. Conversely, though more than a quarter of the Japanese group shared oblong and bottle shapes, there was only a single Japanese/Kuril genotype with this association.

5.2.4.5 Comparison of Japanese/Russian with Foundation Germplasm

Similarly, the variety of fruit shapes in the Japanese/Russian group was generally anticipated based on their parental foundation groups. All fruit shapes found in the Japanese/Russian group were also in one or both parental groups, excepting a single observation of pod shapes that is likely a developmental abnormality (**Section 5.2.4.9**). In specific, bottle, oblong, ovate and spindle shapes were found in both parental groups, while cylindrical and torpedo shapes were seen in the Japanese group and bell shapes in the Russian group. The most important association of shapes was between cylindrical and oblong shapes, which was a principal association in the Japanese but not the Russian group, resulting from a lack of cylindrical shapes in the latter. The associations of ovate with oblong in nearly half the Japanese genotypes and ovate with cylindrical in more than a quarter of the Japanese and Russian genotypes were each seen in

155

tenth of Japanese/Russian genotypes. Bottle and ovate shapes coincided in the Japanese and Japanese/Russian groups but not the Russian group. The obvious relationship between bottle and oblong shapes in the Japanese and Russian groups, as well as bottle and cylindrical shapes in the Japanese group alone, were reflected in many Japanese/Russian genotypes. The association of torpedo with oblong shapes in the Japanese group was also seen in the Japanese/Russian group, but torpedo and bottle shapes were not observed together. Pear shapes being absent in the Japanese group, the association of pear with oblong shapes was seen in both the Russian and Japanese/Russian groups as was the association between bell and bottle shapes. Other minor associations of $2°$ shapes (i.e., bells, pears and pods) were found sporadically in the Japanese/Russian group but did not reflect observations in the parental foundation germplasm.

5.2.4.6 Comparison of Kuril/Russian with Foundation Germplasm

As for the other improved groups, the assortment of shapes found in the Kuril/Russian group resembled expectations from the Kuril and Russian groups. The Kuril/Russian group's oblong and ovate shapes were represented in both parental groups, whereas its cylindrical shapes were only detected in the Kuril group. The improved group's bell, bottle, pear and spindle shapes were found in the Russian group, but torpedo shapes were not found in either parental group. The Kuril/Russian group's predominant association between oblong and cylindrical shapes was only seen in its Kuril parent group due to the lack of cylindrical shapes in the Russian group. Associations of oblong with ovate and ovate with cylindrical shapes were universal in the Kuril group, but only the former was present in the Russian and Kuril/Russian groups. The Kuril/Russian group's more moderate associations of oblong with pear and bottle shapes were seen in its Russian parent group, but its association of cylindrical and bottle shapes was not reflected in either foundation group. Spindle shapes were associated with ovate, oblong and bottle shapes, while bottle shapes were seen with bell shapes in the improved group and its parent groups but too sporadically for interpretation.

5.2.4.7 Comparison of Foundation and Improved Germplasm

The most important $1°$ fruit shapes in the improved germplasm were oblong and cylindrical (29.0% each), followed by ovate (11.0%) and bottle (10.3%) (**Table 5.10**). Torpedo (5.8%), pear (5.2%) and bell (2.6%) shapes were less common, and spindles were not a $1°$ fruit shape. Oblong

was the most prevalent 2° shape (21.9%) with some ovate and bottle shapes (11.6% each). There were minor representations of cylindrical and pear (8.4% each), bell (7.1%), torpedo (4.5%) shapes and rare spindle and pod shapes (1.3 and 0.6%, respectively). Combined, oblong shapes were found in a slim majority (51.0%) of improved genotypes and cylindrical in more than a third (37.4%), followed in prevalence by ovate (22.6%), bottle (21.9%), pear (13.5%), torpedo and bell (9.7% each) and spindle and pod shapes (1.3 and 0.6%, respectively).

Oblong was the most prevalent shape in both the foundation and improved germplasm, more regularly as a 1° than 2° shape. Cylindrical shapes were the second most pervasive 1° shape in the foundation germplasm and were as ubiquitous as oblong 1° shapes in the improved germplasm. Relatively lower prevalence as 2° shapes in both the foundation and improved germplasm made cylindrical shapes the second most important overall. Ovate shapes were the third most common 1° shape in the foundation germplasm and were equal in prevalence to oblong as 2° shapes, resulting in just as many overall occurrences as cylindrical shapes. With moderate prevalence as both 1° and 2° shapes in the improved germplasm, ovate shapes were the third most widespread overall, but were not nearly as common as cylindrical shapes. Bottle shapes were the fourth most common 1° shapes in the foundation germplasm and equally widespread as 2° shapes as oblong and ovate, resulting in an overall prevalence near that of ovate and cylindrical shapes. Similarly, in the improved germplasm, moderate prevalence as both 1° and 2° shapes resulted in nearly the same overall prevalence as ovate shapes. The least observed shapes were torpedo, bell, pear, spindle and pod shapes. Torpedo and bell shapes were only found as 1° shapes in the foundation germplasm; however, they were both 1° and 2° shapes in the improved germplasm. Also, pear shapes were found as 2° shapes in the foundation germplasm and as both 1° and 2° shapes in the improved germplasm, the opposite being true of spindle shapes. Only a single pod shape was found, showing up in the improved germplasm.

Ovate and oblong shapes were detected across all foundation and improved groups. Cylindrical shapes were discovered in the Japanese and Kuril groups but not the Russian or any improved group. Bottle shapes were found in the Japanese and Russian groups but not the Kuril or any improved group. Correspondingly, spindle shapes were found in the Japanese and Russian groups but not the Kuril group, whereas there were only single instances in the Japanese/Russian and Kuril/Russian groups and none in the Japanese/Kuril group. Torpedo shapes were found in only the Japanese foundation group but were seen in all three improved groups. Bell and pear

shapes were only found in the Russian foundation group but were observed in all three improved groups, notably as only $2°$ shapes in the Japanese/Kuril group.

5.2.4.8 Proximal and Distal End Shapes

For all three improved groups, the most wide-spread $1°$ and $2°$ proximal end shapes were rounded and truncate, acute shapes being relatively rare (**Table 5.12; Appendix C.7**). Each improved group reflected expectations based on its respective parental foundation groups: Truncate shapes, followed by rounded, were the most important proximal end shapes for the Japanese/Kuril group and acute proximal end shapes were rare, reflecting their complete absence in both the Japanese and Kuril groups. The Japanese/Russian group's mostly rounded and truncate shapes related to predominance of the former in the Russian and latter in the Japanese group.

The Kuril/Russian group was like the Japanese/Russian group, having slightly more rounded than truncate proximal end shapes as expected from the Kuril and Russian groups. Therefore, as seen in the improved germplasm, the Japanese and Kuril groups are sources of rounded and acute proximal end shapes and the Russian group contributes mostly rounded and some acute shapes.

Rounded $1°$ distal end shapes were most widespread across all three improved groups followed by indented shapes in the Japanese/Russian and Kuril/Russian groups and by flat shapes in the Japanese/Kuril group (**Table 5.12**; **Appendix C.8**). As for proximal end shapes, distal end shapes in the improved groups mirrored expectations from their parental foundation groups. Generally, descending order in prevalence of rounded, indented, flat and peaked shapes was seen in for both the foundation and improved germplasm. Notably, peaked shapes were found in the Japanese/Russian group more often than the other improved groups, reflecting their presence in the Russian and Japanese groups but not the Kuril group.

5.2.4.9 Characterization of Blue Honeysuckle Fruit Shapes

Ovate fruit shapes require a restricted set of end shape combinations: a rounded or truncate proximal end shape with noticeable tapering toward a rounded distal end shape (**Figure 5.7**). Tapering toward the distal end differentiates them from oblong shapes, which are rounded at both ends without tapering. With rounded distal end shapes, ovate shapes either have a completely closed or small opening at the distal end, generally without a rolling lip to the outer accessory layer

Table 5.12. Foundation and Improved Germplasm: Proportions of 1° and 2° proximal and distal fruit end shapes in blue honeysuckle in 2012/2013 in Chilliwack, BC, Canada.

Proximal End Shapes

	Japanese			Kuril			Russian		
	1°	2°	All	1°	2°	All	1°	2°	All
Acute							62.5%		62.5%
Rounded	45.5%	27.3%	72.7%	100.0%		100.0%	100.0%		100.0%
Truncate	100.0%		100.0%	100.0%		100.0%	12.5%		12.5%

	Japanese/Kuril			Japanese/Russian			Kuril/Russian		
	1°	2°	All	1°	2°	All	1°	2°	All
Acute	5.0%	2.5%	7.5%	11.3%	3.8%	15.0%	1.3%	2.5%	3.8%
Rounded	37.5%	25.0%	62.5%	56.3%	16.3%	72.5%	52.5%	8.8%	61.3%
Truncate	70.0%	2.5%	72.5%	50.0%	13.8%	63.8%	43.8%	10.0%	53.8%

Distal End Shapes

	Japanese			Kuril			Russian		
	1°	2°	All	1°	2°	All	1°	2°	All
Flat	9.1%	45.5%	54.5%	20.0%		20.0%			
Rounded	72.7%	9.1%	81.8%	100.0%		100.0%	62.5%	12.5%	75.0%
Indented	54.5%	18.2%	72.7%	80.0%		80.0%	37.5%	25.0%	62.5%
Peaked	27.3%		27.3%				37.5%		37.5%

	Japanese/Kuril			Japanese/Russian			Kuril/Russian		
	1°	2°	All	1°	2°	All	1°	2°	All
Flat	20.0%	12.5%	32.5%	16.3%	11.3%	27.5%	18.8%	8.8%	27.5%
Rounded	60.0%	15.0%	75.0%	50.0%	20.0%	70.0%	48.8%	11.3%	60.0%
Indented	12.5%	25.0%	37.5%	41.3%	12.5%	53.8%	35.0%	12.5%	47.5%
Peaked	5.0%	5.0%	10.0%	7.5%	7.5%	15.0%	3.8%	1.3%	5.0%

	Ovate	Torpedo	Oblong	Cylindrical
Proximal-end:	Rounded, truncate	Rounded, truncate	Rounded	Truncated
Tapering:	Toward distal end	Toward distal end	None	None
Distal-end:	Rounded	Peaked	Rounded	Flat, indented
Opening:	Closed to small	Closed to small	Closed to small	Closed to large

	Bell	Pear	Bottle	Spindle
Proximal-end:	Rounded, truncate	Acute, rounded, truncate	Acute, rounded, truncate	Acute, rounded, truncate
Tapering:	Toward distal end	Toward proximal end	Toward distal end	Toward both ends
Distal-end:	Rounded	Rounded	Flat, indented	Flat, indented
Openings:	Closed to small	Closed to small	Medium to large	Medium to large

Figure 5.7. Foundation and Improved Germplasm: Gross morphological features of different blue honeysuckle fruit shapes in 2012/2013 in the Chilliwack, BC, Canada.

(**Section 5.2.6.3**). The difference between completely closed distal ends and a small opening is that the fruit inside are relatively shorter than the outer accessory layer in the latter case, resulting in detachment of the outer layer from the calices within. When there is a small fruit opening, the distal end resembles a "mail-box slot" with calices withdrawn to the interior. If the calices are not withdrawn, a portion of the fruit often bulges from the accessory capsule's distal end, which is visually unattractive and susceptible to damage during harvest and results in bleeding of fruit juice during handling.

Similarly, torpedo shapes have a rounded or truncate proximal end shape but taper toward a peaked rather than rounded distal end shape. The distal end of these fruit may be completely closed, but a small opening without rolling of the outer accessory layer is also common. When the calices are withdrawn from the peaked distal end, it resembles "bird beak". When the calices are not withdrawn, they jut out from the distal end and are susceptible to damage as for ovate shapes.

Pear (i.e., obovate) shapes are the opposite of ovate shapes, having a rounded distal end shape and an acute, rounded or truncate proximal end shape with noticeable tapering toward the proximal end. In other words, the fruit is larger at the distal end than the proximal. Usually the outer layer is in close contact with the calices, but if a small distal end opening is present, the interior fruit tissues will bulge from within.

Oblong (i.e., elliptical) shapes are restricted to a few end shape combinations and limited distributions of the fruit within the accessory layer. The fruit are rounded at both the distal and proximal ends and do not taper to either end, as is seen for ovate or pear shapes. With rounded distal ends, oblong fruit usually have a closed distal end. As for ovate and torpedo shapes, there may be a small distal end opening that will resemble a "mail-box slot", when the calices are withdrawn, or present a bulge of fruit from the distal end of the accessory layer otherwise.

As for oblong, cylindrical (i.e., elongated) shapes do not taper to either end but have truncate proximal end shapes and either flat or indented distal end shapes. As an important source of within-genotype variation, the association between cylindrical and oblong shapes is due to the abruptness with which the ends terminate. The distal opening is either completely closed, as for flat distal end shapes, or medium to large, as for indented distal end shapes that have a rolled edge. Similarly, bell shapes have rounded proximal ends, as for oblong shapes, and flat or indented distal

161

ends, as for cylindrical shapes, but they are tapered to neither end. Depending on fruit width, the distal opening of bell shapes may be medium or large as for cylindrical shapes.

Bottle shapes have various combinations of end shapes, their proximal ends being acute, rounded or truncate and their distal ends being flat or indented. These shapes are defined by the portion of the fruit closest to the pedicel being broader than the potion nearest the distal end and the transition between these two parts being more abrupt compared to the smooth tapering of ovate shapes. Proximal end shapes are most often rounded and distal end shapes are usually indented with a rolled edge and medium to large distal opening, depending on fruit width. Less commonly, flat distal ends without a rolled edge result in completely closed distal openings relating to the equivalent length of the accessory and fruit tissues. Spindle shapes can have the same diversity of proximal and distal end shape combinations as for bottle shapes. In contrast, both the proximal and distal portions of the fruit are narrower than a bulging central portion with an abrupt transition between these sections rather than the smooth tapering seen for oblong shapes. Like bottle shapes, the principal proximal end shapes are rounded and distal end shapes are indented with a rolled edge and medium to large distal opening, depending on the width of the spindle. Medium openings are apparently more common for spindle than bottle shapes because of how much narrower the fruit tend to be toward the distal end.

Finally, pod shapes manifest randomly as a developmental abnormality of relatively elongated fruit shapes. Upon inspection, a pod-shaped fruit are often missing one of its two fruit or have inconsistent pollination resulting in unequal size of the two fruit within. One flower of each pair opens slightly before the other, explaining the differential in pollination and fruit set. In other cases, the problem appears related to unbalanced growth of the outer accessory layer. In consequence of maladaptive early phenology, development at low temperatures is the probable cause of such developmental abnormalities (**Section 4.2.3.6**). Consequently, pod shapes are associated with poor development, which is why they were not found as a $1°$ shape in any genotypes in the current study. This suggests that pod shapes are not a stand-alone genetic feature but an environmentally-mediated developmental malformation of other shapes related to a lack of phenological adaptation.

5.2.4.10   Associations between Blue Honeysuckle Fruit Shapes

Oblong, ovate and cylindrical shapes are the most widespread and are associated with one another (**Table 5.13**) (**Section 5.2.3**). Association between these three most common shapes was ubiquitous in Kuril group. In the Japanese group, each combination was associated in a quarter to a half of genotypes and most genotypes had one or more of these associations. In all cases where these associations did not exist, cylindrical and bottle shapes were associated. No cylindrical shapes were found in the Russian group, but the only observation of ovate shapes was in association with oblong shapes. This group had a variety of combinations, including oblong with bottle, oblong with pear, bell with bottle and spindle with bottle.

In the improved germplasm, the associations of ovate with cylindrical, oblong with cylindrical and ovate with oblong were universally present but less pronounced in general. These associations were strongest in the Japanese/Kuril group (25.0, 31.3 and 34.4%, respectively). The Japanese/Russian group had more prevalent association of oblong with cylindrical shapes (29.7%) than of ovate with cylindrical or of ovate with oblong shapes (12.5 and 10.9%, respectively), which was expected since no Russian genotypes had cylindrical shapes and only one had ovate shapes. The Kuril/Russian group's strong association between oblong and cylindrical shapes (23.7%) was expected based on parent group observations.

Associations between ovate, oblong and cylindrical shapes in both the foundation and improved germplasm are related to environmentally-mediated variation in the relative lengths of the external accessory tissues and the internal fruit tissues. Oblong shapes, which were the most prevalent $1°$ and $2°$ shapes in both the foundation and improved germplasm, are rounded at both ends and the fruit within have a consistent width. Cylindrical shapes are a blockier variant of oblong shapes for the Japanese and Kuril groups, likely relating to greater proportional development of the accessory layer at both ends relative to the fruit within, making the proximal end shapes truncate and distal end shapes flat or even indented. Ovate shapes are intermediate between cylindrical and oblong shapes with more similarity to the former at the proximal end and to the latter at the distal end, resulting from or resulting in tapering.

Torpedo shapes were associated with ovate, oblong and cylindrical as well as bottle shapes. Torpedo were $1°$ shapes in two Japanese genotypes, being associated with $1°$ ovate and $2°$ oblong shapes in one and with $2°$ cylindrical and bottle shapes in another. Across the three improved groups, torpedo shapes were associated with ovate and/or oblong shapes and, to a lesser degree,

Table 5.13. Foundation and Improved Germplasm: Proportion of genotypes with each association of fruit shapes in blue honeysuckle in 2012/2013 in the Chilliwack, BC, Canada.

All Foundation (24 Genotypes)

	Ovate	Torpedo	Oblong	Cylindrical	Bell	Pear	Bottle	Spindle
Torpedo	4.2%							
Oblong	45.8%	4.2%						
Cylindrical	33.3%	4.2%	37.5%					
Bell								
Pear			4.2%					
Bottle	4.2%	4.2%	20.8%	20.8%	4.2%			
Spindle	4.2%		8.3%				8.3%	
Pod								

All Improved (155 Genotypes)

	Ovate	Torpedo	Oblong	Cylindrical	Bell	Pear	Bottle	Spindle
Torpedo	7.1%							
Oblong	14.8%	7.7%						
Cylindrical	11.0%	1.9%	27.7%					
Bell	0.6%		5.2%	3.6%				
Pear	1.3%		10.3%	6.5%	2.6%			
Bottle	4.5%	0.6%	12.3%	12.9%	3.2%	0.6%		
Spindle						0.6%	0.6%	
Pod			0.6%	0.6%				

All Germplasm (179 Genotypes)

	Ovate	Torpedo	Oblong	Cylindrical	Bell	Pear	Bottle	Spindle
Torpedo	6.7%							
Oblong	19.0%	7.3%						
Cylindrical	14.0%	2.2%	29.1%					
Bell	0.6%		4.5%	3.4%				
Pear	1.1%		9.5%	5.6%	2.2%			
Bottle	4.5%	1.1%	13.4%	14.0%	3.4%	0.6%		
Spindle	0.6%		1.1%			0.6%	1.7%	
Pod			0.6%	0.6%				

cylindrical and/or bottle shapes. Association of torpedo shapes with oblong, ovate and cylindrical shapes is similar to the association of ovate with oblong and cylindrical shapes. If the factors that lead to a more tapered distal end are accompanied by relatively greater elongation of the outer accessory layer in conjunction with relatively short fruit within, a peaked distal end will result in a torpedo shape overall. Correspondingly, the association between torpedo and bottle shapes is due to the opposite shift in fruit morphology where there is an elongation of the proximal end of the fruit, resulting in a more bulbous mass of fruit near the distal end.

Bottle shapes were associated with oblong and cylindrical as well as ovate shapes. In the foundation germplasm, over half of the genotypes with bottle shapes also had oblong and cylindrical shapes. Bottle shapes were $2°$ to torpedo shapes in a single Japanese genotype, whereas ovate shapes were $2°$ to bottle shapes in another. Similarly, approximately half of improved genotypes with bottle shapes also had oblong and cylindrical shapes, while ovate and torpedo shapes were only occasionally seen in the same genotype, never sharing $1°$ shape status. These trends illustrate that bottle shapes are a more extreme intermediate form between oblong and cylindrical shapes to what is seen for ovate and torpedo shapes. While the development of the accessory tissue is relatively greater than the fruit within for the distal end of the ovate and torpedo shapes, this is exaggerated in bottle shapes.

Bell and pear shapes were associated with oblong, cylindrical and bottle shapes. In the foundation germplasm, the single observations of pear and bell shapes showed associations with oblong and bottle shapes, respectively. Oblong shapes accompanied half of improved genotypes with bell shapes, while a third were combined with cylindrical and bottle shapes. Similarly, oblong shapes were associated in two thirds of genotypes with pear shapes, and cylindrical and bottle shapes were associated in a third and quarter of genotypes with pear shapes, respectively. As they were not associated in the foundation germplasm, it was unsurprising that less than a fifth of bell and pear shapes were associated in the improved germplasm. As modifications of the basic oblong and cylindrical shapes, bell shapes can be considered an open-ended form of pear shapes. Bell shapes are characterized by an over-developed part of the accessory layer at the proximal end more than a relative imbalance in the distribution of fruit toward the distal end. Pear shapes are characterized by a relative imbalance in the distribution of fruit toward the distal end more than over-development of the accessory layer toward the proximal end.

Spindle shapes were associated with oblong, ovate and bottle shapes in the foundation germplasm and with pear and bottle shapes in the improved germplasm, manifesting as an even more extreme modification from the basic shapes than bottle shapes. Particularly, spindle shapes have an imbalanced distribution of the fruit tissues as well as an over-development of the distal end of the accessory layer, as for bottle shapes, but the accessory layer also juts out past the distal end of the fruit, resulting in a secondary tapering. Since they were associated with oblong, ovate and bottle shapes in the foundation germplasm, this is clearly a compound modification of basic oblong and cylindrical shapes. In the foundation germplasm, spindle shapes were $2°$ in one Japanese genotype with $1°$ oblong and bottle shapes, whereas they were $2°$ to oblong and ovate shapes in one Russian genotype and $1°$ in another genotype that had $2°$ bottle shapes. In the improved germplasm, one Japanese/Russian genotype had $2°$ spindle shapes with $1°$ pear shapes and one Kuril/Russian genotype had $2°$ spindle shapes with $1°$ bottle shapes. Therefore, the association of spindle shapes with oblong, ovate, bottle and pear shapes demonstrates an extreme modification of the basic shapes with a secondary restriction at the distal end.

Blue honeysuckle fruit shape varies resulting in response to modifications in three aspects of the fruit's morphology: the length of the accessory layer relative to the fruit within; the distribution of the fruit within the accessory layer; and the way in which the accessory layer terminates at the distal end, relating to its proximity to the fruit tissue within, the size of the distal opening and the presence or absence of a rolled edge of accessory tissue. Variations in the environmental and nutritional factors that have direct effects on the processes of fruit development lead to heterogeneity in both fruit shape and size within genotypes (**Section 5.2.5.4** and **5.3.6.4**). For example, a genotype with mostly oblong shapes may also have some torpedo shapes due to factors that result in either relatively longer accessory tissues, shorter fruit structures or both. Equally, a genotype with mostly ovate or torpedo shapes may also have some bottle shapes resulting from environmental factors that lead to in more extended fruit tissues relative to the accessory layer. Therefore, diversity in the combinations and relative proportions of fruit shapes is found across both the foundation and improved germplasm, between and within specific germplasm groups and even within harvests of individual genotypes. This diversity is evidence of the polygenic control of fruit shape in blue honeysuckle.

5.2.5   Qualitative Measures of Agronomic Potential in Foundation Germplasm
5.2.5.1 Incomplete Fruit Synanthy and Evenness of Fruit Synanthy

Incomplete fruit synanthy is a developmental abnormality caused by failure of the bracts of the cupula to fully enclose the tip of the fruit, which permits the ovary walls to show from within (Thompson 2006a). These abnormalities vary in appearance, with either a quarter or half of the sheath being curled back or missing completely, and they result from the freedom of the margin of the bracteolar sheath from the ovary walls (Rehder 1903). It is sometimes caused by triple flowering (i.e., reversion to a three-flowered cyme), but more often occurs in consequence of poor pollination or damage to the accessory tissue during development (**Section 5.2.3.6**). These malformations make the fruit both visually unattractive to potential consumers and make the fruit susceptible to damage and post-harvest rot during harvest, sorting and packing. Of individual fruit harvests, incomplete synanthy was seen in nearly half for the Japanese group, a third for the Russian group and a tenth for the Kuril group (**Table 5.14; Appendix C.9**). Incidence ranged from about a tenth of harvests (J-41-83) to more than three quarters in J-43-87 and J-66-53 for the Japanese group; from none (R-2-07 and R-2-10) to nearly every harvest (R-2-11) for the Russian group; and from none (K-3-06 and K-3-07) to a tenth (K-3-03 and K-3-05) to half (K-97-12) for the Kuril group. Incomplete synanthy was observed for a tenth of J-PP harvests and between two fifths and two thirds of harvests for the U of S cultivars.

Similarly, blue honeysuckle presents a range in surface smoothness that relates to positioning of the fruit within the accessory layer. An uneven fruit surface is undesirable for commercial production because it has the potential to increase susceptibility to bruising, impede rolling on a sorting belt and to be visually unappealing to the end consumer. Fruit surface ratings were most uneven (i.e., bumpy) for the Russian group, followed by the Japanese and then the Kuril group. Russian and Japanese groups were 'smooth' (R-2-13 and J-73-39) to 'very bumpy' (R-2-14 and J-21-78), while the Kuril group was most often 'slightly bumpy' and occasionally 'smooth', without any clear difference between genotypes. J-PP was 'smooth' to 'slightly bumpy', as was 'Indigo Gem', but 'Borealis' and 'Tundra' were 'slightly bumpy' to 'moderately bumpy'.

Variation in fruit synanthy and evenness of surface in the Japanese and Russian groups will permit selection of suitable breeding parents for these traits. The Kuril group is the best genetic source for complete synanthy and evenness of fruit surface, but K-97-12 was the parent for the three U of S cultivars, which all had high incidences of incomplete synanthy. This suggests the

Table 5.14. Foundation Germplasm: Proportion of fruit harvests receiving each agronomic rating for blue honeysuckle in 2012/2013 in the Fraser Valley, BC, Canada (n=18).

Fruit Synanthy	Japanese	Kuril	Russian
Complete	50.5%	88.1%	66.7%
Incomplete	49.5%	11.9%	33.3%

Fruit Colour	Japanese	Kuril	Russian
Dark blue	25.5%	58.5%	70.8%
Purplish-blue	50.0%	41.5%	16.7%
Bluish-purple	24.5%	0.0%	12.5%

Fruit Bloom	Japanese	Kuril	Russian
Very heavy	36.4%	2.4%	60.4%
Heavy	25.3%	11.9%	29.2%
Moderately heavy	23.2%	28.6%	6.3%
Moderate	11.1%	28.6%	4.2%
Dull	0.0%	14.3%	0.0%
Very dull	4.0%	11.9%	0.0%
Minimal	0.0%	2.4%	0.0%

Fruit Shape in Cross-Section	Japanese	Kuril	Russian
Circular	13.3%	0.0%	37.5%
Broad elliptic or circular	42.9%	2.4%	10.4%
Broad elliptic	37.8%	9.5%	37.5%
Narrow or broad elliptic	3.1%	47.6%	6.3%
Narrow elliptic	3.1%	40.5%	8.3%

Fruit Surface	Japanese	Kuril	Russian
Smooth	18.4%	28.6%	8.3%
Slightly bumpy	53.1%	71.4%	20.8%
Moderately bumpy	19.4%	0.0%	31.3%
Bumpy	3.1%	0.0%	14.6%
Very bumpy	6.1%	0.0%	25.0%

Fruit Pubescence	Japanese	Kuril	Russian
Absent	73.7%	26.2%	64.6%
Minimal	2.0%	4.8%	0.0%
Very slight	24.2%	54.8%	20.8%
Slight	0.0%	0.0%	0.0%
Moderately low	0.0%	0.0%	14.6%
Moderate	0.0%	0.0%	0.0%
Moderately high	0.0%	0.0%	0.0%
High	0.0%	0.0%	0.0%
Very high	0.0%	14.3%	0.0%

Distal Opening Size	Japanese	Kuril	Russian
Closed	9.4%	92.9%	39.6%
Very small	44.8%	4.8%	2.1%
Small	7.3%	2.4%	0.0%
Medium-small	16.7%	0.0%	4.2%
Medium	17.7%	0.0%	31.3%
Medium-large	4.2%	0.0%	6.3%
Large	0.0%	0.0%	16.7%

Table 5.14. Continued. Foundation Germplasm: Proportion of fruit harvests receiving each agronomic rating for blue honeysuckle in 2012/2013 in the Fraser Valley, BC, Canada (n=18).

Heterogeneity of Fruit Size	Japanese	Kuril	Russian
Minimal	2.5%	17.2%	3.4%
Slight	12.7%	28.7%	17.9%
Moderate	46.7%	27.6%	50.4%
High	33.5%	21.8%	23.9%
Very high	4.6%	4.6%	4.3%

Heterogeneity of Fruit Shape	Japanese	Kuril	Russian
Minimal	6.1%	19.8%	3.4%
Slight	19.8%	23.3%	15.5%
Moderate	44.2%	30.2%	43.1%
High	23.9%	26.7%	30.2%
Very high	6.1%	0.0%	7.8%

Fruit Taste	Japanese	Kuril	Russian
Sweet	13.2%	2.4%	5.6%
Sour-sweet	11.7%	18.8%	23.4%
Sweet-sour	26.4%	55.3%	30.8%
Sour	6.6%	3.5%	0.9%
Very sour	15.2%	12.9%	15.9%
Astringent	26.9%	7.1%	20.6%

Fruit Aroma	Japanese	Kuril	Russian
Very high	2.1%	0.0%	15.7%
High	24.2%	10.5%	18.6%
Moderately high	35.6%	34.9%	27.5%
Moderate	17.0%	27.9%	24.5%
Slight	13.4%	25.6%	8.8%
Very slight	5.2%	1.2%	4.9%
Minimal	2.6%	0.0%	0.0%

Fruit Flesh Firmness	Japanese	Kuril	Russian
Very firm	8.7%	6.9%	20.2%
Firm	20.9%	20.7%	26.9%
Doughy	21.4%	27.6%	24.0%
Doughy-soft	24.5%	34.5%	9.6%
Soft	16.8%	9.2%	10.6%
Very soft	6.1%	1.1%	5.8%
Watery	1.5%	0.0%	2.9%

Fruit Mold	Japanese	Kuril	Russian
None	85.9%	60.0%	97.2%
Minimal	6.1%	17.8%	1.4%
Moderate	3.0%	15.6%	1.4%
Severe	5.1%	6.7%	0.0%

Table 5.14. Continued. Foundation Germplasm: Proportion of fruit harvests receiving each agronomic rating for blue honeysuckle in 2012/2013 in the Fraser Valley, BC, Canada (n=18).

Strength of Fruit Attachment	Japanese	Kuril	Russian
Extremely loose	14.8%	0.0%	0.0%
Very loose	12.2%	3.5%	1.7%
Loose	9.7%	8.1%	8.6%
Moderately loose	14.8%	8.1%	6.9%
Moderate	20.4%	29.1%	28.4%
Moderately tight	7.7%	33.7%	19.0%
Tight	9.7%	12.8%	22.4%
Very tight	7.1%	3.5%	7.8%
Extremely tight	3.6%	1.2%	5.2%

Stem Retention in Harvest	Japanese	Kuril	Russian
None	34.8%	14.9%	31.9%
Very slight	14.1%	11.5%	10.3%
Slight	29.8%	35.6%	25.0%
Moderate	3.5%	2.3%	10.3%
Moderately high	12.6%	26.4%	19.8%
High	0.5%	0.0%	0.0%
Very high	4.5%	9.2%	2.6%

Picking Scar Quality	Japanese	Kuril	Russian
Small and dry	62.9%	25.3%	50.4%
Small and wet	8.6%	73.6%	11.3%
Large and dry	24.4%	1.1%	20.0%
Large and wet	4.1%	0.0%	18.3%

need to choose parents with a low tendency to contribute this trait and to select against it in improved populations.

5.2.5.2 Fruit Pubescence, Bloom and Colour

Blue honeysuckle fruit pubescence most often projects from the end of the fruit, arising from the ovary wall near the calyx margin, but it can also be seen on the surface of the cupula. These fine trichomes are usually imperceptible to the mouth during fruit consumption, but even their appearance may be visually unappealing to the consumer. The Japanese group had the least pubescent fruit, followed closely by the Russian group, whereas the Kuril group was skewed by the most hirsute genotype, K-97-12 (**Table 5.14**; **Appendix C.9**). Ratings ranged from 'absent' to 'very slight' (J-42-25, J-43-87 and J-56-18) for the Japanese group and from 'absent' to 'moderately low' for the Russian group, only R-2-13 and R-27-35 having any noticeable degrees of pubescence. For the Kuril group, the four late genotypes (**Section 4.2.1.1**) were rated between 'absent' and 'very slight', but K-97-12 was rated as 'very high'. Consequently, 'Borealis' had a 'moderately high' rating and 'Tundra' and 'Indigo Gem' had 'high' ratings. J-PP had no observable pubescence.

Covering the nearly black epidermal layer of the fruit cupula, the waxy cuticle (i.e., bloom) creates the characteristic sky blue (i.e., caerulean) colour of the fruit. A thicker cuticle results in a heavier bloom and lighter overall appearance that is attractive to most consumers. A heavy cuticle may also be associated with decreased water loss after harvest or resistance to fungal pathogens, resulting in better shelf life. Fruit bloom was heaviest for the Russian group, lower for the Japanese group and lower still for the Kuril group. Ratings ranged from 'moderate' to 'very heavy' for the Russian group, R-2-06, R-2-07 and R-2-16 being rated as 'very heavy' and R-27-35 having the lowest rating; from 'very dull' to 'very heavy' for the Japanese group, J-21-78, J-42-45, J-43-87, J-444-39 and J-56-18 having higher ratings and J-45-14 a lower rating; and from 'dull' to 'very heavy' for the Kuril group but most often 'moderate' to 'moderately heavy', K-97-12 having the heaviest average bloom rating. 'Tundra' had a similar rating to the Russian average, and 'Borealis' and 'Indigo Gem' were better and worse than the Kuril average, respectively. J-PP had a 'moderately heavy' rating, which was close to the Japanese average.

Beneath the bloom, fruit with consistently dark blue fruit colour appear riper and are more appealing to the consumer than fruit with purplish or reddish flesh. Fruit colour was most

171

consistently 'dark blue' for the Russian group, more often lighter in colour for the Japanese group and intermediate for the Kuril group. R-2-07, R-2-13, R-2-14 and R-2-16 were rated as 'dark blue' for all harvests, while R-27-25 stood out with the poorest rating. Though Japanese harvests were most often rated as 'dark blue' (e.g., J-22-14), there were quite a few 'bluish-purple' observations (e.g., J-66-53 and J-45-14). Half of Kuril harvests were rated as 'purplish-blue' and the remaining were evenly split between 'dark blue' and 'bluish-purple'. J-PP had a slightly worse rating than the average Japanese genotype. 'Borealis' was considerably lighter than either the average Russian or Kuril genotypes. 'Tundra' and 'Indigo Gem' were mostly 'dark blue'.

At the U of S, fruit pubescence ratings on all Russian genotypes included in the current study except R-27-35, showed a low correlation (r = 0.38) with these findings, suggesting an environmental influence on this trait. This is reflected in the inconsistency with which observation of pubescence were made across harvests of the four late Kuril genotypes. In contrast, for K-97-12, heavy pubescence was observed in every harvest, which undoubtedly detracts from this genotype's agronomic potential. The Russian and Japanese groups are the best sources for a low degree of pubescence and heavy bloom, while selection against pubescence and weak bloom is required when using Kuril material in breeding. Case in point, the high degree of pubescence in the U of S cultivars, and contrastingly acceptable bloom ratings, can be traced to their female parent (K-97-12), suggesting that Kuril material can be used with careful selection of breeding parents. For fruit colour, there was important variation in the Japanese and Russian groups, presenting opportunities for genetic improvement, and the Kuril group had consistently moderate ratings that do not diminish this group's utility in future crossing strategies.

5.2.5.3 Fruit Shape in Cross-Section and Opening Size

The presence of two fruit inside the cupula results in variability in width both parallel and perpendicular to the frontal plane (**Sections 5.3.1.1** and **5.3.2.2**). Variability in the ratio between these dimensions results in either round or elliptic shape in cross-section, the former being an important trait for ease of rolling during machine harvest and sorting. Fruit shape in cross-section was similar for the Japanese and Russian groups compared with the narrower Kuril group (**Table 5.14**; **Appendix C.9**). Ratings were mostly 'broad elliptic' to 'broad elliptic or circular' for the Japanese group and split between 'broad elliptic' and 'circular' for the Russian group, observations ranging across the whole scale in both cases. J-46-55 and J-41-83 had the broadest and narrowest

172

ratings in the Japanese group. R-2-13 and R-2-07 were the broadest and R-2-14 and R-2-10 were the narrowest in the Russian group. The Kuril group had little variability with mostly 'narrow elliptic' or 'narrow or broad elliptic' but never 'circular' ratings. J-PP was relatively narrow compared to the Japanese group, whereas 'Indigo Gem' was broader than any Russian or Kuril genotype. 'Borealis' and 'Tundra' were moderate compared to the Russian group but more circular than K-97-12.

Rolling is also effected by the size of the distal end opening (**Sections 5.3.6.6** and **5.3.4.9**). Though future back-yard cultivars may include an assortment of fruit opening sizes with accompanying ranges in fruit size and shape, commercial production will benefit from a small or closed distal end. Distal opening size was smallest on average for the Kuril group's oblong, cylindrical and ovate shapes (**Section 5.2.3.2**) with virtually all ratings being 'closed' without a rolled edge or withdrawal of the calices from the edge of the accessory tissue. The Japanese group most often had 'very small' openings without a rolled edge but with redaction of the calices from the accessory tissue (e.g., J-41-83, J-42-45, J-43-87 and J-73-39 had ovate, torpedo, cylindrical and oblong shapes with rounded distal ends), but observations ranged as high as 'medium-large' with a rolled edge (e.g., J-56-18, J-46-55 and J-21-78 that were primarily bottle shaped with indented distal end shapes) (**Section 5.2.3.1**). The Russian group ranged from 'closed' to 'medium' and 'large'. The phenotypic average for the Russian group was larger than the intermediate Japanese, but the median was substantially higher than the average because of downward skew. R-2-11, R-2-13 and R-27-35 were the Russian genotypes with little to no opening, which was associated with their mostly oblong shapes with rounded distal ends (**Section 5.2.3.3**). R-2-06, R-2-16, R-2-10, R-2-14 and R-2-07 all had average ratings between 'medium' and 'medium-large', which were associated with bottle, spindle and bell shapes in addition to the basic oblong shapes. In comparison, J-PP had a 'small' to 'medium-small' distal opening size to accompany its mostly oblong shapes and rounded distal end shapes. 'Indigo Gem' had 'closed' to 'very small' distal opening size and oblong, pear or ovate shapes with rounded distal end shape. 'Borealis' and 'Tundra' had 'medium-small' distal openings, which were associated with mostly oblong, cylindrical and some bottle and pear shapes. Though their distal ends were mostly flat or rounded, indented were also observed.

In Saskatchewan, Russian fruit are noted for their relatively narrow shape in cross-section, experimental comparison of 17 cultivars showing 15% lower measurements in parallel to the

frontal plane compared to perpendicular (Bors et al 2012). The widths in this study (parallel to the frontal plane) were not correlated with the current findings (r = 0.10), which show that both the Japanese and Russian groups are considerable sources of wider cross-sectional shapes, whereas the Kuril group is relatively narrow, which detracts from agronomic potential. The potential for fruit quality (FQ) issues associated with larger fruit opening sizes in some Russian and Japanese genotypes is offset by the degree of variability within these groups, but the Kuril group possesses the best source of closed distal ends. Breeding toward novelty (e.g., large distal openings) in fruit shapes for home gardens must be secondary to development of cultivars suited to large-scale production, but both the Japanese and Russian groups hold potential in this regard. For commercial production, a smaller distal opening for 'Indigo Gem' is a positive feature compared to 'Borealis' and 'Tundra'.

5.2.5.4 Heterogeneity in Fruit Size and Shape

As a multiple accessory fruit, blue honeysuckle has a unique fruit morphology (**Section 5.2.3.6**), which leads to a wide diversity of fruit shapes and sizes not just between and within genetic groups, but within harvests of individual genotypes (**Section 5.2.4.9**). This variation is related to environmentally-mediated transitions between closely related fruit shapes that are modifications of a few basic fruit shapes (**Section 5.2.4.10**), which relate to parameters of fruit size such as weight, length and width both in parallel and in perpendicular to the frontal plane (**Sections 5.3.1.5**; **5.3.2.7** and **5.2.5.3**). A low degree of heterogeneity in fruit size is important from a mass-market perspective because of the influence of size on key components of FQ (**Section 6.2.1.4**) and nutritional content (**Section 6.2.2.4**). Similarly, low heterogeneity in fruit shape is important for consistency in traits such uniform ripening, physical integrity during harvest, ability to roll on sorting lines and predictability and consistency of quality parameters for processed products.

Ratings for heterogeneity in fruit size and shape were very similar, showing normal distributions across the foundation germplasm, which suggests polygenic control (**Table 5.14**; **Appendix C.9**). For both traits, heterogeneity in Japanese and Russian harvests was most often rated as 'moderate', while Kuril harvests were more evenly spread across 'minimal' to 'high' with slightly more uniform averages overall. For the Japanese group, J-56-18 had the highest heterogeneity in both size and shape. For the Kuril group, K-97-12 was more often heterogeneous

for size but not shape. For the Russian group, a more continuous distribution of genotypes was seen, with R-2-10, R-2-11 and R-2-13 having the three highest degrees of heterogeneity in size and R-2-07, R-2-10 and R-27-35 the highest heterogeneity in shape. J-PP and the three U of S cultivars had primarily 'moderate' heterogeneity in fruit size and shape, which was close to the Russian group's average but lower than for K-97-12.

With similar ranges across groups, selection of parents that contribute uniformity of fruit size and shape is a matter of within-group selection and should be possible using any of the three foundation groups, perhaps especially with the Kuril group.

5.2.5.5 Fruit Taste and Aroma

Ratings for blue honeysuckle fruit taste were based primarily on a subjective evaluation of the ratio between sweetness and sourness, which relate to TSS and TA and pH (**Sections 6.2.1** and **6.2.3**). Blue honeysuckle is known for its bitterness in the wild, but none of the genotypes included in the current trial bore this trait as it was selected against during domestication. Sweeter taste ratings were considered positive from an agronomic standpoint as tart to astringent fruit tend to have more limited mass-market appeal for fresh consumption and limitations for processed product applications. 'Sweetish-sour' is the most common fruit taste in Russian germplasm and is accompanied by slight fruit aroma (Kolasin and Pozdynakov 1991). Therefore, though one of blue honeysuckle's appealing features is the tartness it contributes to processed and value-added products, the fruit must have a milder overall taste to gain wide-spread commercial acceptance (Thompson 2006a).

The average fruit taste was quite similar for the Japanese and Russian groups, ranging from 'sweet' to 'astringent' but being 'sour' on average (**Table 5.14; Appendix C.9**). For the Kuril group, more than half of harvests were rated as 'sweetish-sour' but ranged from 'sweet' to 'astringent' as for the other two groups. The average for the Kuril group was slightly sweeter than for the Japanese and Russian groups. The range in phenotypic averages was broadest for the Russian group and narrowest for the Kuril group, while it was relatively intermediate for the Japanese group. Therefore, the sweetest and sourest genotypes were both seen in the Russian group, while the Japanese group's extremes were still more sweet and more sour than the extremes of the Kuril group. Within the Japanese group, J-22-14, J-66-53 and J-73-39 were 'very sour', whereas J-45-14 was between 'sourish-sweet' and 'sweetish-sour'. For the Kuril group, K-97-12

175

was 'sour' to 'very sour' and the four late genotypes were quite consistently 'sweetish-sour'. For the Russian group, R-2-13, R-27-35 and R-2-14 were 'astringent' or worse though R-2-07 and R-2-16 received the sweetest average ratings of all genotypes, 'sourish-sweet' and 'sweetish-sour', respectively. In comparison, J-PP was slightly more sour than the average Japanese genotype. 'Borealis' was like K-97-12 and the average Russian rating between 'sour' and 'very sour'. 'Tundra' and 'Indigo Gem' were slightly milder, 'sweetish-sour' to 'sour'.

In connection to the sensations of taste and smell, the strength and concentration of aromatic compounds function to inform flavour. Intensity of fruit aroma is, therefore, an important facet of marketability of both fresh and processed products. Fruit aroma ratings followed an approximately normal distribution for the three foundation groups, and the greatest proportion of each group received 'moderately high' ratings. The Japanese group included ratings across the entire length of the scale, there were no high or low extremes observed for the Kuril group. All except the lowest extreme were observed for the Russian group. The phenotypic average was only slightly higher for the Russian group than the Japanese group, which was higher than for the Kuril group, but the spread of phenotypic averages was greater for the Japanese group than the Russian and Kuril groups. The absolute lowest rating was found in the Japanese group (J-444-39) and highest in the Russian group (R-2-16), whereas the Kuril group's highest rating (K-97-12) was similar to the Russian group's lowest (R-2-13). J-PP was relatively unaromatic compared to the other Japanese genotypes, receiving an average rating slightly below 'moderate'. 'Indigo Gem', 'Borealis' and 'Tundra' were rated 'moderately high' or better, which was equivalent to the Kuril group's average but lower than for most of the Russian group.

Optimum ripeness, the point at which fruit taste should be evaluated, is reached a few to several days after full ripening (Nakajima 1996; Prischepina 2000), but weather conditions prior to harvest have a major impact on development of blue honeysuckle flavour (Murslimova 2013). Therefore, climatic differences during fruit ripening impact the perception of taste and aroma. In Saskatchewan, J-22-14 is noted as the best tasting Japanese genotype (Bors et al 2012), but in the temperate climate of the current study, this genotype had one of the sourest fruit taste ratings in the Japanese group. For Russian germplasm, evaluations in the southern Urals indicate R-2-07 and R-2-10 have a 'sweetish-sour' taste (Murslimova 2013), which is close to the ratings received in the Fraser Valley. In Saskatchewan, R-2-10 and R-2-13 had two of the best fruit aromas in the material used in early breeding efforts at the U of S (Bors 2009), this being observed for similar

the former and not the latter in the current study. Also, 'Borealis' is described as "sweet tart", 'Tundra' as "sweet tangy" and 'Indigo Gem' as "sweet" in Saskatchewan (Bors 2009), which are relative subjective descriptions that compare well with the current study. In contrast, 'Borealis' is noted for having better overall aroma than 'Tundra' or 'Indigo Gem' (Bors 2009), which contrasts with evaluations of aroma in the Fraser Valley.

Breeding with Kuril material should provide consistently milder fruit taste than the other groups, but there are opportunities to use the other groups to access the extremes in taste. Conversely, K-97-12 is the only source of strong aroma in the Kuril group, but the Russian group is the best source fruit aroma. Also, there is wide variation in aroma within the Japanese group.

5.2.5.6 Fruit Mold and Firmness of Fruit Flesh

In the Fraser Valley, common fruit rot pathogens include fungal organisms such as *Botrytis* spp. (i.e., grey mold), *Alternaria* spp. (i.e., black mold) and *Colletotrichum acutatum* (i.e., Anthracnose). Without the use of preventative fungicides in the current trial, ratings for the severity of pre-harvest infection by any of these pathogens permitted evaluation of the natural susceptibility of blue honeysuckle genetics, which has inference for potential shelf life. Fruit mold was more often observed during harvest of Kuril than Japanese fruit and least often for Russian fruit (**Table 5.14; Appendix C.9**). Specifically, 60% and 86% of Kuril and Japanese harvests were mold free, respectively, individual observations ranging up to 'severe'. In contrast, Russian harvests were 97% mold-free. The Kuril group did not demonstrate important distinctions between genotypes, even for K97-12. The only 'minimal' and 'moderate' observations in the Russian group were for R-27-35, and J-56-18 had the highest ratings by far in the Japanese group. Of note, both R-27-35 and J-56-18 were late outlier in the Russian and Japanese groups, respectively (**Section 4.2.1.3** and **4.2.1.1**), the former having the highest yield in its group (**Section 5.2.1.4**) and the latter tending to retain its corollas at harvest, which was not noted for any other genotype.

These data demonstrate a close relationship between later phenology (**Section 4.2.1.1**) and more frequent observation of fruit mold. Specifically, the later Kuril group had a higher instance than the Japanese group with intermediate phenology, which had a higher instance than the early Russian group. Also, J-56-18 and R-27-35 were both the latest genotypes and had the greatest incidence of fruit rot within their respective groups. The warm, wet conditions experienced during the latter part of the blue honeysuckle season were likely the driver for differences in mold

incidence rather than any direct genetic susceptibility. Since breeding for phenological adaptation to a temperate climate requires selection of later phenology to ensure optimal pollination (**Section 4.2.1.3**) and productivity (**Section 5.2.1.1**), more prevalent fruit mold is a reality. Selecting against susceptibility to mold may be possible among later genotypes, but the current study does not clearly indicate how this should be achieved and integration of chemical management options may obviate this point.

Rating fruit firmness during taste testing is a subjective assessment that relates to shelf life as well as appeal to consumers as a fresh product, the firmer the better for small fruit in general. Since blue honeysuckle seeds are generally small (3.8 g/1000), they are characteristically imperceptible during fruit consumption (Suchkova and Senina 2009). Therefore, the fruit firmness rated in the current study was primarily related to the resistance of fruit flesh to compression during mastication. Fruit flesh ratings were quite evenly spread from 'firm' to 'doughy-soft' for the Japanese group though there were ratings from 'very firm' to 'watery' for individual harvests. The Kuril group was rated as 'doughy-soft' for a third of harvests with many contrasting 'firm' and 'doughy' ratings and an overall range from 'very firm' to 'very soft'. The Russian group was evenly spread from 'very firm' to 'doughy' with some ratings reaching to the 'watery' extreme. The phenotypic average was softest for the Japanese group, which was followed closely by the Kuril group, while the Russian group was considerably firmer. The firmest (R-2-10) and softest (R-27-35) extremes were both found in the Russian group, respectively. The Kuril group had the narrowest range in firmness, but K-97-12 was firmer than the four late genotypes. J-41-83, J-43-39 and J-42-45 varied from 'firm' to 'doughy', whereas J-56-18, J-444-39 and J-73-39 reached from 'doughy-soft' to 'soft'. J-PP and 'Indigo Gem' had 'soft' fruit flesh, softer than any other Japanese genotype. 'Borealis', with a 'very soft' average rating, was even softer than R-27-35. 'Tundra' had a firmer rating than any of the Japanese or Kuril genotypes (including K-97-12) and was only surpassed by R-2-10 and R-2-16 in the Russian group.

No germplasm evaluations for susceptibility to fruit mold are available in the literature, but several authors indicate the potential to produce blue honeysuckle using organic or low-input practices. Observationally, the low incidence of fruit mold compared to other crops in the current study suggests that blue honeysuckle may have a low tendency to develop pre-harvest fruit rot in a temperate climate. This finding should be treated cautiously as no quantitative comparison was made with the comparison crops. Additionally, there is the potential for disease issues to develop

over time with increasing prevalence of pathogen strains that are suited to infecting the newly introduced crop with accompanying buildup of inocula.

In Saskatchewan, firmness ratings on all Russian genotypes included in the current study, except for R-27-35, showed a low correlation (r = 0.313) with this data (Bors et al 2012), whereas no evaluations for the Japanese or Kuril groups are available for comparison. Yet, 'Borealis' was considered too fragile for mechanical harvest, 'Tundra' was noted for its firmer flesh and 'Indigo Gem' was described as "chewy" (Bors 2009). In the Fraser Valley, 'Tundra' was the firmest and 'Borealis' was the least firm, the more intermediate rating for 'Indigo Gem' perhaps relating to the toughness of its skin and reflecting its "chewy" texture. Principally, this study shows that the Japanese group is the most consistent source of fruit firmness, but the Russian group has the greatest extremes in firmness for use in breeding. The firm Russian fruit were also considerably smaller than most in the Japanese and Kuril groups, and selection for larger fruit size is an important priority for increasing productivity (**Section 5.2.1.6**). Therefore, the Russian group should not be considered the principal source of firmness as the Japanese and Kuril groups contain a range in firmness along with larger fruit sizes. Intense, early selection against the lower firmness that accompanies larger fruit sizes should be employed.

5.2.5.7 Fruit Attachment Strength, Stem Retention and Picking Scar Quality

Harvestability is a multi-faceted trait that includes the strength of fruit attachment to the plant, the degree to which fruit stems (i.e., pedicels) are retained in harvested fruit and the size and integrity of the picking scar. Strength of fruit attachment ranges from spontaneous pre-harvest shattering, a major hurdle in early Russian breeding efforts, to requiring such force as to detach the stems along with the fruit or rip the proximal end of the fruit (Plekhanova 1989). Fruit stems are a harvest contaminant for both fresh and processed end uses, and a scar that is large or wet (i.e., that bleeds fruit juice) or both will cause rapid loss of firmness during handling and storage. Both mechanical and manual harvest require loose fruit attachment to the plant, a low tendency for stems to detach during harvest and a small, dry picking scar. These aspects of harvestability are related to synchrony of fruit ripening over the entire plant for which genetic variability is observed in Corvallis, OR (Thompson 2006a).

Strength of fruit attachment varied from 'very loose' to 'extremely tight' for the Kuril group but was more often rated as 'moderately tight' or 'moderate' with a generally normal

distribution of observations (**Table 5.14; Appendix C.9**). The Russian genotypes most often had 'moderate' ratings with a high proportion of 'moderately tight' and 'tight' ratings and a total spread from 'very loose' to 'extremely tight'. Japanese harvests were evenly spread across the rating scale with more ratings in the 'moderate' and 'moderately loose' categories. On average, attachment was tighter for the Kuril and Russian groups than for the Japanese group. J-73-39 and R-27-35 had the tightest attachment, with ratings between 'very tight' and 'extremely tight', and J-21-78 had the loosest rating. For the Kuril group, K-97-12 was a little easier to detach than the four late genotypes, which had 'moderate' to 'moderately tight' attachment. Variation in attachment strength was very narrow for the Kuril group, moderate for the Russian group and broad for the Japanese group. J-PP had one of the tightest attachments, and was more difficult to detach than all but J-73-39 in the Japanese group. 'Borealis' had 'very tight' attachment, making it worse than all genotypes except for J-73-39 and R-27-35. 'Tundra' had 'tight' attachment and 'Indigo Gem' had slightly looser attachment on average, but both were tighter than all Kuril and most Russian and Japanese genotypes.

Contamination of fruit harvests with stems was highest for the Kuril group, with ratings between 'slight' and 'moderate', while the Japanese and Russian groups were typically between 'very slight' and 'slight'. All three foundation groups contained harvests rated from 'none' to 'very high', but the phenotypic range was broader for the Japanese than the Kuril group, which was broader than the Russian group. The highest and lowest average ratings were for Japanese genotypes (J-21-78 and J-41-83, respectively), whereas the Kuril group had a moderate range resulting from low incidence of stem contamination for K-97-12 compared to the four late genotypes. The Russian group had the narrowest range, from 'very slight' (R-2-07) to 'moderately high' (R-2-06, R-27-35 and R-2-11). J-PP had an average rating compared to the Japanese group. 'Borealis' had a much greater degree of stem contamination compared to the other U of S cultivars and was equivalent to some of the worst Japanese genotypes. 'Tundra' and 'Indigo Gem' had relatively low levels of contamination with average ratings between 'none' and 'very slight'.

Picking scar quality was scored as 'small and dry' for almost two thirds of Japanese harvests and another quarter as 'large and dry' with less than a tenth as 'small and wet' and 'large and wet' combined. For the Kuril group, nearly three quarters of ratings were 'small and wet', while a quarter were 'small and dry' and only 1% were 'large and dry'. For the Russian group, half of harvests had 'small and dry' and a fifth had 'large and dry' picking scars, whereas a tenth

and a fifth had 'small and wet' and 'large and wet' scars, respectively. Parsing these ratings, picking scars were three quarters 'small' and nearly nine tenths 'dry' in the Japanese group. Almost all picking scars were 'small' in the Kuril group, but three quarters were 'wet'. Slightly more than two thirds of picking scars were 'small' and slightly less than a third were 'dry' in the Russian group. In comparison, picking scars were most often 'small and dry' for J-PP, primarily 'large and dry' for 'Borealis' and most often 'small and wet' for 'Tundra' and 'Indigo Gem'.

The potential for completely synchronous harvest of all fruit on each blue honeysuckle plant is a major advantage compared to crops such as blueberry, raspberry and strawberry, which require multiple harvests (**Section 4.2.1.2**). Reports on Russian material in several cold Eurasian climates indicate that multiple harvests are necessary to avoid pre-harvest shattering (Gawroński et al 2014; Murslimova 2013; Korobkova 2009), while difficult detachment was noted as a challenge in Japanese material in Corvallis, OR (Thompson and Barney 2007). No considerable pre-harvest shattering was observed in the Fraser Valley because phenology was used to determine harvest date for individual plants (**Section 4.2.1.1**). The loosest attachment strength ratings present the greatest opportunity to improve harvestability for a temperate climate. In the Fraser Valley, the Japanese group is the best source of loose fruit attachment, but the Russian group contains some useful variability as well. This differs from observations in Saskatchewan's cold climate where the Russian group had looser fruit attachment than the Japanese group (Bors 2009). Evaluation of attachment strength at the U of S for all Russian genotypes included in the current study, except for R-27-35, was not correlated with these findings (r = 0.060) (Bors et al 2012).

The Japanese group is the best source for a low degree of harvest contamination with detached stems, but this group also has the greatest phenotypic variation for this trait. The Kuril genotypes were most often contaminated, but K-97-12 stood out for having fewer stems accompanying harvested fruit, likely relating to the Russian group's moderate degree of contamination. The Japanese group also provide the most consistent source of scars that are both 'small and dry' with some tendency for larger scars but little tendency for wet scars. However, the Kuril group contributes a scar that often bleeds though it is consistently small. The Russian group possesses a range of scar types, half of which are the desirably 'small and dry'. Environmental influences on picking scar quality are suggested since the findings for 'Borealis' and 'Tundra' in Saskatchewan (Bors 2009) were opposite to the findings of the current study.

181

5.2.5.8 Selection Index

Summing the range standardize ratings (0 to 1) for agronomic potential with equal weights for each trait, the relative selection index (SI) demonstrated a slightly better phenotypic average for the Japanese than the Russian group, which had a better phenotypic average than the Kuril group (**Figure 5.8**; **Appendix C.10**). The Russian group showed some negative skew, contrasting with the Japanese and Kuril groups, which demonstrated positive skew. More importantly, the range differed across groups: The Russian group contained the genotypes with the best and worst SI scores, whereas the range for the Japanese and Kuril groups were three quarters and only a tenth as broad, respectively. Therefore, variability in agronomic potential was an order of magnitude greater for the Russian than the Kuril group. However, variability in the Japanese group being nearly as great as in the Russian group.

The SI highlighted the most important traits that contributed to, and detracted from, agronomic potential for each group (**Figure 5.9**). The Japanese group's average was positively influenced, in order of importance, by lack of pubescence, loose fruit attachment, circular fruit shape in cross-section, and good picking scar quality. In contrast, it was reduced by light fruit colour, prevalence of incomplete synanthy and heterogeneity of fruit size. The Kuril group's average benefited from closed distal ends, even fruit surface, complete synanthy, good picking scar quality, uniform fruit size and shape and sweet fruit taste. It was reduced by narrow shape in cross-section, dull bloom, presence of pubescence, pre-harvest mold and stems retained at harvest as well as a weak aroma. The Russian group's average was positively impacted by lack of pubescence, dark blue colour, complete synanthy, heavy bloom, relatively round shape in cross-section, firm flesh, infrequent presence of mold and strong fruit aroma. It was reduced by large openings at the distal end, uneven fruit surface, tight attachment to the plant, relatively sour fruit taste, poor picking scar quality and heterogeneity of fruit shape.

5.2.6 Qualitative Measures of Agronomic Potential in Improved Germplasm
5.2.6.1 Incomplete Fruit Synanthy and Evenness of Fruit Surface

'Incomplete' fruit synanthy was less prevalent in fruit harvests for the Japanese/Kuril and Kuril/Russian groups (22 and 24%, respectively) than for the Japanese/Russian group (34%) (**Table 5.15**; **Appendix C.11**). All three improved groups contained genotypes for which all individual harvests were devoid of 'incomplete' synanthy as well as genotypes for which every
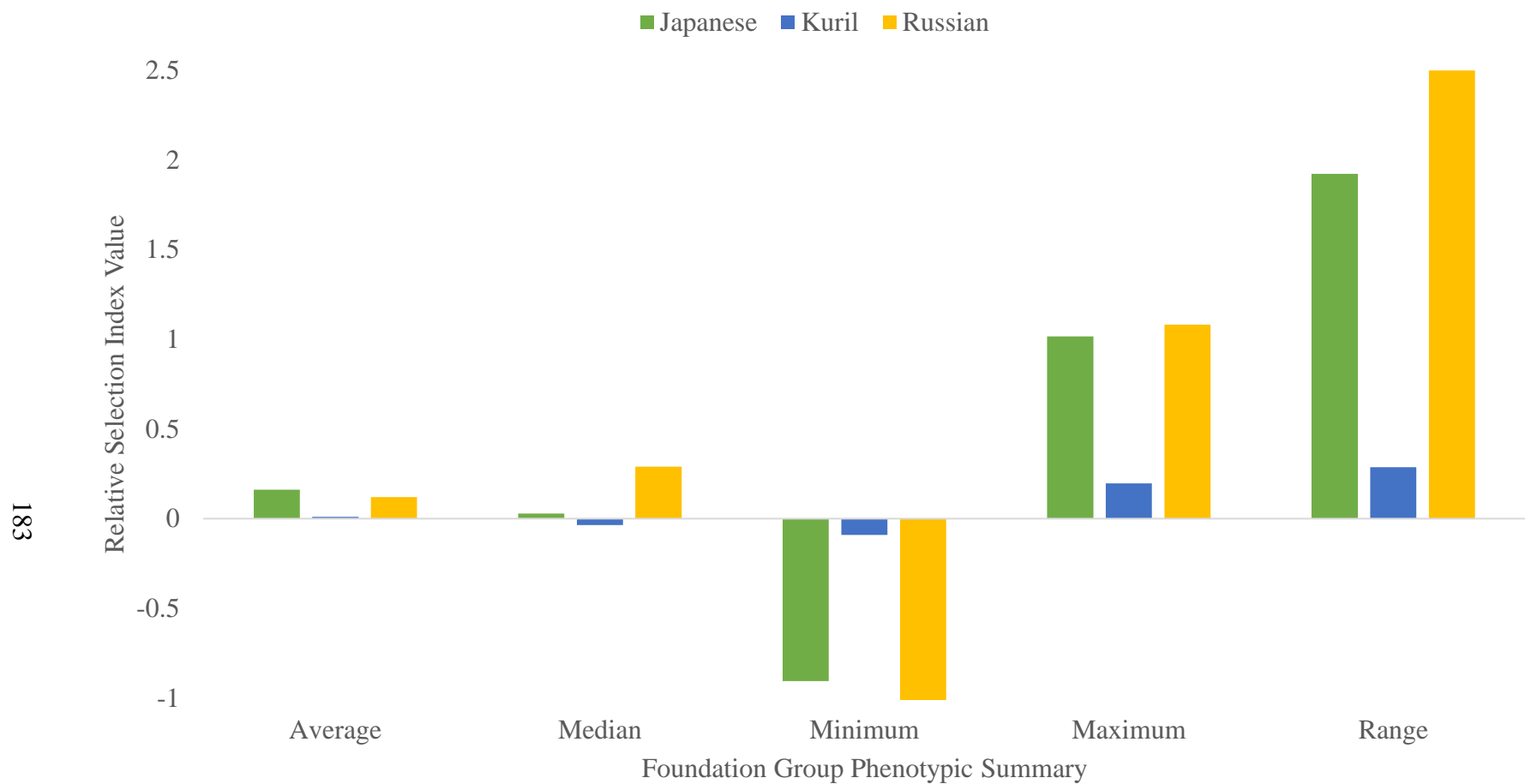
Figure 5.8. Foundation Germplasm: Phenotypic summary of relative selection index for 16 fruit agronomic ratings for blue honeysuckle in 2012/2013 in the Fraser Valley, BC, Canada.
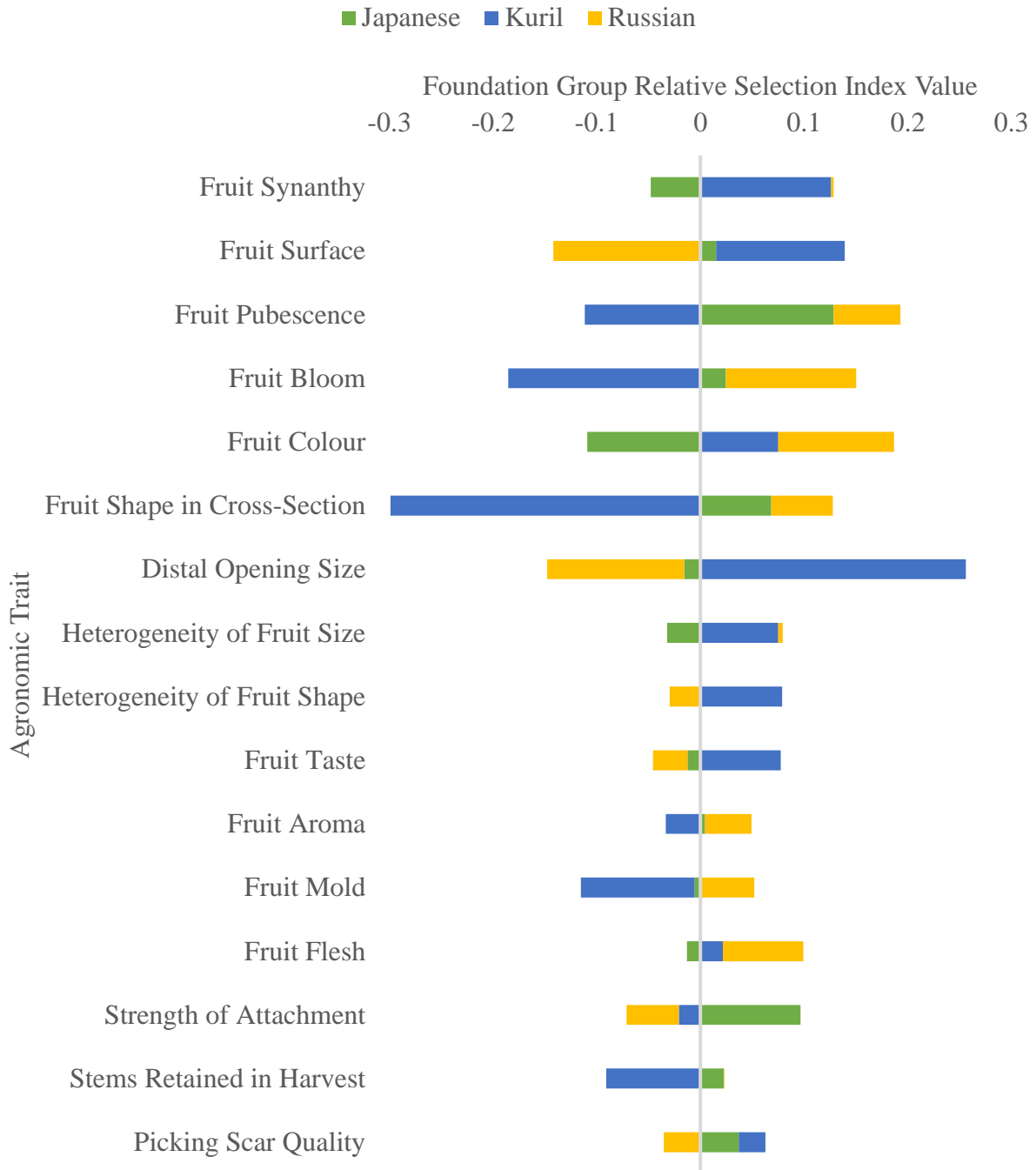
Figure 5.9. Foundation Germplasm: Effects of 16 fruit agronomic ratings on a relative selection index for blue honeysuckle in 2012/2013 in the Fraser Valley, BC, Canada.

harvest contained fruit with 'incomplete' synanthy. In the foundation groups, this former extreme was only seen for the Kuril and Russian groups, whereas the latter extreme was not seen in any group. The Japanese/Russian and Japanese/Kuril groups had phenotypic averages intermediate to their respective parent groups, but the average for the Kuril/Russian group was higher than for either of its parent groups. H^2 was moderate in the foundation and improved germplasm combined and separately and in the Japanese and Kuril groups on their own, while it was very high for the Russian group, high for the Japanese/Kuril and Japanese/Russian groups and low for the Kuril/Russian group. In contrast, h^2 was low across the improved germplasm and only in the Japanese/Kuril group on its own (**Table 5.16**).

Evenness of fruit surfaces ranged from 'smooth' to 'bumpy' for Japanese/Kuril harvests but were most often 'smooth' to 'slightly bumpy'. The average was intermediate to the averages of its parent groups though skewed toward the smoother Kuril group. Japanese/Russian harvests ranged from 'smooth' to 'very bumpy' but most often 'slightly bumpy'. The average was intermediate to its parent groups but skewed toward the smoother Japanese group. Kuril/Russian fruit were 'smooth' to 'very bumpy', having a similar distribution to the Japanese/Russian group and averaging between the relatively smooth Kuril and bumpy Russian groups. All three improved groups contained genotypes with perfect 'smooth' ratings at one extreme that contrasted with genotypes that were almost as bumpy as the extreme observations in their respective parent groups. H^2 was high across the foundation and improved germplasm combined and separate and in each group on its own except for the Kuril and Russian groups for which it was moderate and low, respectively. While low across the improved germplasm combined, h^2 was only considerable for the Japanese/Russian and Kuril/Russian groups on their own.

To select against the incidence of incomplete synanthy while breeding with the Japanese group, crossing with either the Russian or Kuril group should permit genetic progress with probable additive gains in crosses between the Japanese and Russian groups. Genetic progress is least likely in crosses between the Russian and Kuril groups. For evenness of fruit surfaces, additive genetic gains in crosses with the Russian group are related to the greater degree of unevenness in this group. While additive gene action will permit selection against bumpiness in crosses using the Russian group, breeding for greater evenness will be more attainable using the evenly surfaced Japanese and Kuril groups. This is supported by observation of greater evenness of fruit surfaces for the Japanese/Kuril group than the other improved groups.

Table 5.15. Foundation and Improved Germplasm: Proportion of fruit harvests receiving each agronomic rating for blue honeysuckle in 2012/2013 in Chilliwack, BC, Canada (n=18).

Fruit Synanthy		Japanese	Kuril	Russian	Japanese/ Kuril	Japanese/ Russian	Kuril/ Russian
Fruit Synanthy	Complete	64.0%	83.8%	88.9%	77.5%	66.2%	76.5%
	Incomplete	36.0%	16.2%	11.1%	22.5%	33.8%	23.5%
Fruit Surface	Smooth	22.5%	31.6%	22.2%	33.5%	21.1%	18.9%
	Slightly bumpy	50.6%	65.8%	7.4%	53.7%	47.7%	46.7%
	Moderately bumpy	18.0%	2.6%	29.6%	11.0%	22.2%	25.3%
	Bumpy	7.9%	0.0%	3.7%	1.8%	7.4%	6.3%
	Very bumpy	1.1%	0.0%	37.0%	0.0%	1.5%	2.8%
Fruit Pubescence	Absent	68.5%	26.3%	63.0%	33.5%	59.0%	57.9%
	Minimal	0.0%	0.0%	0.0%	3.5%	3.7%	2.5%
	Very slight	30.3%	55.3%	25.9%	48.0%	30.5%	24.6%
	Slight	0.0%	0.0%	0.0%	3.5%	1.1%	1.1%
	Low moderate	1.1%	2.6%	11.1%	11.0%	4.8%	10.5%
	Moderate	0.0%	0.0%	0.0%	0.4%	0.2%	0.4%
	Moderately high	0.0%	15.8%	0.0%	0.0%	0.7%	3.2%
Fruit Bloom	Very heavy	21.3%	2.6%	33.3%	15.0%	20.9%	22.1%
	Heavy	34.8%	5.3%	29.6%	32.3%	36.2%	43.5%
	Moderately heavy	21.3%	31.6%	7.4%	31.0%	32.0%	23.5%
	Moderate	9.0%	50.0%	7.4%	18.6%	8.7%	7.4%
	Dull	9.0%	10.5%	22.2%	3.1%	1.7%	2.8%
	Very dull	4.5%	0.0%	0.0%	0.0%	0.4%	0.7%
	Minimal	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%
Fruit Colour	Dark blue	27.0%	57.9%	77.8%	30.0%	30.6%	56.8%
	Purplish-blue	46.1%	42.1%	18.5%	45.8%	43.2%	29.5%
	Bluish-purple	27.0%	0.0%	3.7%	24.2%	26.2%	13.7%

Table 5.15. Continued. Foundation and Improved Germplasm: Proportion of fruit harvests receiving each agronomic rating for blue honeysuckle in 2012/2013 in Chilliwack, BC, Canada (n=18).

		Japanese	Kuril	Russian	Japanese/ Kuril	Japanese/ Russian	Kuril/ Russian
Fruit Shape in Cross-Section	Circular	15.9%	0.0%	25.9%	16.3%	17.6%	6.3%
	Broad elliptic or circular	48.9%	5.4%	11.1%	26.0%	27.0%	14.8%
	Broad elliptic	30.7%	43.2%	40.7%	42.3%	43.6%	29.6%
	Narrow or broad elliptic	4.5%	24.3%	7.4%	11.9%	10.2%	22.5%
	Narrow elliptic	0.0%	27.0%	14.8%	3.5%	1.5%	26.8%
Distal Opening Size	Closed	5.6%	54.1%	44.4%	44.1%	24.0%	29.2%
	Very small	47.2%	8.1%	0.0%	24.7%	16.8%	7.4%
	Small	21.3%	21.6%	25.9%	12.3%	18.7%	16.5%
	Medium-small	14.6%	13.5%	7.4%	13.2%	19.4%	20.8%
	Medium	11.2%	2.7%	7.4%	4.0%	13.9%	19.7%
	Medium-large	0.0%	0.0%	0.0%	1.8%	3.5%	2.8%
	Large	0.0%	0.0%	14.8%	0.0%	3.7%	3.5%
Heterogeneity of Fruit Size	Minimal	2.1%	10.0%	3.7%	1.8%	1.6%	1.7%
	Slight	24.1%	31.3%	24.4%	15.1%	20.3%	18.3%
	Moderate	43.3%	23.8%	48.8%	50.3%	49.2%	51.1%
	High	25.1%	30.0%	11.0%	29.8%	23.2%	24.9%
	Very high	5.3%	5.0%	12.2%	3.0%	5.7%	4.0%
Heterogeneity of Fruit Shape	Minimal	2.7%	17.5%	1.2%	1.8%	1.9%	1.2%
	Slight	19.8%	23.8%	23.2%	26.8%	18.9%	20.4%
	Moderate	48.7%	20.0%	39.0%	41.1%	39.5%	41.8%
	High	24.6%	37.5%	19.5%	25.8%	32.2%	30.6%
	Very high	4.3%	1.3%	17.1%	4.6%	7.5%	5.9%

Table 5.15. Continued. Foundation and Improved Germplasm: Proportion of fruit harvests receiving each agronomic rating for blue honeysuckle in 2012/2013 in Chilliwack, BC, Canada (n=18).

		Japanese	Kuril	Russian	Japanese/ Kuril	Japanese/ Russian	Kuril/ Russian
Fruit Taste	Sweet	14.7%	0.0%	4.9%	8.9%	10.8%	6.8%
	Sourish-sweet	32.1%	51.3%	29.5%	34.1%	29.3%	27.8%
	Sweetish-sour	23.4%	35.5%	14.8%	26.7%	30.0%	25.4%
	Sour	29.3%	10.5%	50.8%	29.1%	28.1%	38.2%
	Very sour	0.5%	0.0%	0.0%	0.0%	0.2%	0.0%
	Astringent	0.0%	2.6%	0.0%	1.2%	1.5%	1.9%
Fruit Aroma	Very high	3.3%	0.0%	3.3%	0.8%	2.5%	1.7%
	High	11.5%	3.9%	6.7%	11.3%	10.8%	9.3%
	Moderately high	27.3%	48.7%	23.3%	32.7%	33.8%	27.4%
	Moderate	27.3%	35.5%	25.0%	32.1%	28.6%	26.1%
	Slight	17.5%	10.5%	21.7%	17.6%	18.1%	27.1%
	Very slight	9.3%	1.3%	16.7%	4.8%	4.8%	6.9%
	Minimal	3.8%	0.0%	3.3%	0.6%	1.4%	1.5%
Fruit Mold	None	81.6%	48.9%	92.2%	82.6%	79.6%	84.6%
	Minimal	8.2%	26.7%	3.1%	10.3%	12.2%	12.2%
	Moderate	3.1%	15.6%	4.7%	4.6%	4.5%	2.6%
Fruit Flesh Firmness	Very firm	6.5%	6.6%	21.3%	9.3%	5.7%	7.2%
	Firm	16.8%	15.8%	26.2%	17.4%	7.7%	9.7%
	Doughy	34.8%	31.6%	19.7%	29.1%	28.3%	24.7%
	Doughy-soft	23.9%	32.9%	8.2%	21.8%	20.9%	19.3%
	Soft	12.5%	13.2%	18.0%	16.2%	21.3%	23.3%
	Very soft	3.8%	0.0%	6.6%	5.5%	10.9%	10.4%
	Watery	1.6%	0.0%	0.0%	0.8%	5.1%	5.5%

Table 5.15. Continued. Foundation and Improved Germplasm: Proportion of fruit harvests receiving each agronomic rating for blue honeysuckle in 2012/2013 in Chilliwack, BC, Canada (n=18).

		Japanese	Kuril	Russian	Japanese/ Kuril	Japanese/ Russian	Kuril/ Russian
Strength of Fruit Attachment	Extremely loose	7.5%	1.3%	9.5%	14.1%	6.3%	2.2%
	Very loose	9.7%	0.0%	17.9%	10.5%	10.7%	7.8%
	Loose	11.3%	10.0%	14.3%	13.3%	12.9%	11.6%
	Moderately loose	22.6%	17.5%	7.1%	15.4%	17.6%	15.5%
	Moderate	18.8%	36.3%	26.2%	25.7%	20.4%	20.1%
	Moderately tight	8.6%	20.0%	6.0%	13.1%	16.2%	21.0%
	Tight	12.9%	8.8%	8.3%	5.7%	9.7%	14.5%
	Very tight	8.1%	2.5%	6.0%	1.8%	2.8%	6.2%
	Extremely tight	0.5%	3.8%	4.8%	0.4%	3.3%	1.1%
Stems Retained in Harvest	None	55.6%	10.0%	26.2%	45.1%	39.5%	30.3%
	Very slight	4.3%	23.8%	16.7%	21.8%	21.0%	19.7%
	Slight	28.9%	35.0%	19.0%	23.2%	23.2%	23.3%
	Moderate	5.3%	1.3%	6.0%	3.6%	3.7%	8.0%
	Moderately high	5.9%	25.0%	15.5%	5.3%	9.5%	16.0%
	High	0.0%	0.0%	9.5%	0.2%	0.0%	0.4%
	Very high	0.0%	5.0%	7.1%	0.8%	3.0%	2.2%
Picking Scar Quality	Small and dry	60.4%	30.0%	64.7%	60.2%	61.6%	47.5%
	Small and wet	6.4%	70.0%	3.5%	20.0%	9.0%	19.0%
	Large and dry	28.9%	0.0%	17.6%	15.6%	23.1%	17.5%
	Large and wet	4.3%	0.0%	14.1%	4.2%	6.3%	16.0%

Table 5.16. Foundation and Improved Germplasm: Heritability estimates for agronomic ratings for blue honeysuckle in 2012/2013 in Chilliwack, BC, Canada (H^2 – broad-sense heritability calculated from linear mixed model regression, h^2 – narrow-sense heritability calculated from mid-parent regression on phenotypic averages[1]).

	Fruit Synanthy		Fruit Surface		Fruit Pubescence		Fruit Bloom		Fruit Colour		Fruit Shape in Cross-Section		Distal Opening Size		Heterogeneity of Fruit Size	
	H^2	h^2	H^2	h^2	H^2	h^2	H^2	h^2	H^2	h^2	H^2	h^2	H^2	h^2	H^2	h^2
All Germplasm	0.65	-	0.83	-	0.90	-	0.77	-	0.76	-	0.83	-	0.88	-	0.61	-
All Foundation	0.70	-	0.86	-	0.95	-	0.79	-	0.69	-	0.72	-	0.76	-	0.48	-
Japanese	0.61	-	0.83	-	0.92	-	0.84	-	0.50	-	0.41	-	0.79	-	0.60	-
Kuril	0.62	-	0.55	-	0.96	-	0.83	-	0.55	-	0.56	-	0.44	-	0.20	-
Russian	0.91	-	0.49	-	0.89	-	0.01	-	0.40	-	0.00	-	0.28	-	0.00	-
All Improved	0.65	0.23	0.83	0.35	0.89	0.49	0.75	0.07	0.76	0.20	0.84	0.22	0.88	0.00	0.63	0.04
Japanese/Kuril	0.70	0.15	0.80	0.18	0.86	0.51	0.81	0.49	0.75	0.19	0.76	0.00	0.89	0.02	0.46	0.06
Japanese/Russia	0.74	0.25	0.86	0.38	0.88	0.16	0.67	0.00	0.72	0.00	0.72	0.00	0.86	0.04	0.56	0.18
Kuril/Russian	0.30	0.06	0.72	0.25	0.87	0.57	0.70	0.05	0.70	0.07	0.76	0.06	0.85	0.00	0.68	0.00

[1]Different regression models were used to calculate H^2 and h^2 heritability estimates, so these measures are not directly comparable.

Table 5.16. Continued. Foundation and Improved Germplasm: Heritability estimates for agronomic ratings for blue honeysuckle in 2012/2013 in Chilliwack, BC, Canada (H^2 – broad-sense heritability calculated from linear mixed model regression, h^2 – narrow-sense heritability calculated from mid-parent regression on phenotypic averages[1]).

	Heterogeneity of Fruit Shape		Fruit Taste		Fruit Aroma		Fruit Mold		Fruit Flesh Firmness		Strength of Attachment		Stem Retention in Harvest		Picking Scar Quality	
	H^2	h^2	H^2	h^2	H^2	h^2	H^2	h^2	H^2	h^2	H^2	h^2	H^2	h^2	H^2	h^2
All Germplasm	0.32	-	0.72	-	0.69	-	0.79	-	0.86	-	0.78	-	0.89	-	0.84	-
All Foundation	0.33	-	0.72	-	0.82	-	0.86	-	0.89	-	0.86	-	0.88	-	0.95	-
Japanese	0.76	-	0.64	-	0.87	-	0.98	-	0.79	-	0.88	-	0.92	-	0.93	-
Kuril	0.12	-	0.71	-	0.54	-	0.14	-	0.81	-	0.26	-	0.13	-	0.95	-
Russian	0.00	-	0.70	-	0.52	-	0.81	-	0.94	-	0.81	-	0.01	-	0.81	-
All Improved	0.32	0.10	0.72	0.08	0.67	0.10	0.74	0.00	0.84	0.00	0.77	0.03	0.89	0.21	0.81	0.19
Japanese/Kuril	0.28	0.00	0.77	0.23	0.84	0.30	0.74	0.00	0.87	0.03	0.64	0.00	0.86	0.00	0.92	0.23
Japanese/Russia	0.35	0.12	0.67	0.12	0.64	0.19	0.79	0.12	0.76	0.00	0.80	0.20	0.92	0.26	0.77	0.37
Kuril/Russian	0.25	0.00	0.76	0.00	0.59	0.06	0.58	0.01	0.87	0.03	0.74	0.00	0.84	0.14	0.73	0.03

[1]Different regression models were used to calculate H^2 and h^2 heritability estimates, so these measures are not directly comparable.

5.2.6.2 Fruit Pubescence, Bloom and Colour

Fruit pubescence for Japanese/Kuril fruit ranged from 'absent' to 'moderate', but it was most often 'absent' to 'very slight', which was intermediate to its parent groups (**Table 5.15**; **Appendix C.11**). Pubescence in Japanese/Russian fruit was mostly 'absent' or 'very slight' as for the Japanese/Kuril group, but a few observations reached 'moderately high'. The Japanese/Russian group's average was still intermediate to the similar Japanese and Russian group averages. Kuril/Russian fruit pubescence ranged from 'absent' to 'moderately high' with heavy skewed toward scarce pubescence reflected in a phenotypic average that was much closer to the lower Russian group's average. All three improved groups had genotypes for which no harvest demonstrated any pubescence as was found for the Japanese and Russian groups, but the more pubescent extremes were intermediate between those of their respective parent groups. H^2 was high to very high across the foundation and improved germplasm combined and separate and in each group individually. Across the improved germplasm, h^2 was moderate as for the Japanese/Kuril and Kuril/Russian groups on their own (**Table 5.16**).

The Japanese/Kuril group had fruit bloom ratings from 'dull' to 'very heavy', ratings being mostly 'moderately heavy' or 'heavy' and averaging closer to the heavier bloom of the Japanese group than the dull bloom of the Kuril group. Similarly, for the Japanese/Russian group, ratings ranged from 'very dull' to 'very heavy', were mostly 'moderately heavy' or 'heavy' and averaged slightly heavier than for either of its parent group. For the Kuril/Russian group, ratings ranged from 'very dull' to 'very heavy' but were most often 'heavy' with a heavier average than for even the Russian parent group. Each improved group had similarly heavy and dull extremes in fruit bloom that were also close to those of each foundation group. H^2 was moderate to high across the foundation and improved germplasm combined and separate and in each group on its own except in the Russian group for which it was negligible. h^2 was moderate in the Japanese/Kuril group but negligible in the other improved groups and across the improved germplasm.

Fruit colour ratings for the Japanese/Kuril and Japanese/Russian groups were mostly 'purplish-blue' with about the same proportions of 'dark blue' and 'bluish-purple' ratings and nearly identical averages. In both cases, the averages were much closer to the lighter Japanese group's colour than the darker Kuril or Russian group's colours. The Kuril/Russian group had mostly 'dark blue' ratings, more 'purplish-blue' ratings than 'bluish-purple' and an average that was darker than the other improved groups but lighter than its parent groups. All three improved

groups had genotypes with consistently 'dark blue' ratings, but only the Russian group had genotypes that always received these ratings in the foundation germplasm. The Japanese/Russian and Kuril/Russian groups had genotypes that were universally rated as 'bluish-purple'; the Japanese/Kuril group had genotypes that almost always received this rating; in contrast, no foundation genotype consistently received such light ratings for fruit colour. H^2 was high across the foundation and improved germplasm combined, across the improved germplasm alone and in each improved group individually, while it was moderate across the foundation germplasm and for the Japanese and Kuril groups but low for the Russian group. Negligible h^2 was observed across the improved germplasm and in each improved group on its own.

Considerable genetic gains in reduced fruit pubescence should be possible through crossing the Kuril group with either the Japanese or Russian group. The Kuril group has the least desirable fruit pubescence ratings, which is merely an indication of the potential to select against this trait. The Japanese/Russian group demonstrates lower H^2 because its parent groups have correspondingly low degrees of pubescence, which results in superior ratings in improved genotypes. Whereas additive gains in fruit bloom can be made in crossing the Japanese and Kuril groups, there is an opportunity to generate transgressive segregants for heavier bloom through use of with the Russian group in crosses with Japanese genotypes. In contrast, combination of the Kuril and Russian groups did not demonstrate a considerable degree of H^2 despite the greatest disparity in average group ratings. Since the average rating for each improved group was higher than, or equal to, the highest foundation germplasm group average, dominance or over-dominance of heavier fruit bloom may be observed in future crosses. For fruit colour, additive genetic gains are unlikely, but combination of Russian and Kuril groups will consistently produce darker fruit.

5.2.6.3 Fruit Shape in Cross-Section and Opening Size

The Japanese/Kuril and Japanese/Russian groups were most often ranked as 'broad elliptic', but observations spanned the whole scale with skew toward 'circular' and averages intermediate to their respective parent groups (**Table 5.15; Appendix C.11**). The Kuril/Russian group showed a more even spread of ratings from 'narrow elliptic' to 'broad elliptic' with some more 'circular' ratings as well, which denoted skew toward the narrow Kuril group. All three improved groups had genotypes that were always rated as 'circular', though only the Kuril/Russian group had genotypes with consistently 'narrow elliptic' ratings, not having the relatively 'circular'

Japanese group in their lineage. H^2 was high across the foundation and improved germplasm combined and separate and in each improved group on its own but was moderate, low and negligible for the Kuril, Japanese and Russian groups, respectively. Low h^2 was observed across the improved germplasm, and it was negligible for each improved group on its own (**Table 5.16**).

Most Japanese/Kuril genotypes had completely 'closed' distal fruit openings with a range in ratings that tapered to 'medium-large' and averaged closer to the Kuril group. In contrast, the Japanese/Russian and Kuril/Russian groups displayed more even distributions of distal openings from 'closed' to 'large', but they also had skew toward 'closed' distal ends with larger average openings than their respective parent groups. All three improved groups contained genotypes with consistently 'closed' ratings, but this extreme was not found in any of the foundation groups. Similarly, the largest distal opening in each improved group was larger than in their respective foundation groups, while the most extreme genotypes were in the Kuril/Russian group. H^2 was high across the foundation and improved germplasm combined and separate and in each improved group and the Japanese group on their own, but it was low and negligible for the Kuril and Russian groups, respectively, while h^2 was universally negligible.

Additive genetic gains toward circular shapes in cross-section are unlikely, but selection for this trait will likely be successful in improved populations. The circular shapes of the Japanese group are seemingly moderated by the narrower shapes of the Kuril and Russian groups, these latter two groups combining to produce the narrowest shapes in cross-section. Distal opening sizes in the Japanese/Russian and Kuril/Russian groups suggest dominance or over-dominance of the Russian group's larger openings. Breeding for novel fruit shapes with a range of opening sizes should be possible with the use of the Russian group, but any improved group will likely manifest improved genotypes with consistently closed distal ends desirable for commercial production. Particularly, crossing the Japanese and Kuril groups stands as an opportunity to obtain more closed distal ends, which is likely more to do with dominance from the Kuril group than additive gene action between the two groups.

5.2.6.4 Heterogeneity in Fruit Size and Shape

As for the foundation germplasm, the improved germplasm showed a normal distribution for heterogeneity in both fruit size and shape with the greatest proportions being 'moderate' ratings (**Table 5.15; Appendix C.11**). The average for each improved group was approximately the same

194

as that of its respective parent groups. For heterogeneity in size, the Kuril/Russian group had the widest range, followed by the Japanese/Russian group and then the Japanese/Kuril group, which still had a range slightly greater than any of the foundation groups. For heterogeneity in shape, the range between the highest and lowest improved genotypes was comparatively intermediate to each group's respective parent groups. H^2 for heterogeneity in size was low to moderate across the foundation and improved germplasm combined and separate and in each group on its own except the Kuril and Russian groups for which it was negligible (**Table 5.16**). For heterogeneity in shape, H^2 was low across the foundation and improved germplasm combined and separate and in the Japanese/Russian group, while it was high in the Japanese group and negligible for all other groups on their own. For both heterogeneity in size and shape, h^2 was negligible for the improved groups combined and separate. Therefore, making additive genetic gains in uniformity of fruit size and shape will be difficult, and selection for these apparently quantitative traits will require intense selection in any improved seedling population.

5.2.6.5 Fruit Taste and Aroma

The ranges in fruit taste were quite similar across improved groups, and a third of ratings in each group were seen for 'sourish-sweet', 'sweetish-sour' and 'sour' (**Table 5.15; Appendix C.11**). Each group had genotypes with the most extreme 'sweet' ratings and, to a lesser extent, the 'astringent' extreme. The average for each improved group was close to its parent group averages, but the range of observations was slightly greater for each improved group. H^2 was high across the foundation and improved germplasm combined and separate and in each group on its own except for the Japanese and Japanese/Russian groups for which it was moderate. Low h^2 was detected for the Japanese/Kuril group and it was negligible otherwise (**Table 5.16**).

Fruit aroma ratings approximated a normal distribution for all improved groups, each including observations across the entire spectrum. 'Moderate' to 'moderately high' ratings were the most frequent scores for each improved group, with some skew toward the 'slight' end of the scale, especially in the Kuril/Russian group. Average ratings were similar across improved groups and were equivalent to the Kuril group average. The highest phenotypic average was found in the Japanese group, whereas the highest phenotypic average in the improved germplasm was slightly lower, being found in the Japanese/Kuril group. Extremely low aroma ratings for Japanese/Kuril and Japanese/Russian genotypes were like those found in the Japanese and Russian groups, while

the lowest extreme in the Kuril/Russian group was a consistent rating of 'minimal' aroma. H^2 was moderate to high across the foundation and improved germplasm combined and separate and in each group on its own, whereas h^2 was low for the Japanese/Kuril group and negligible otherwise.

Comparison of open-pollinated and cross-pollinated populations of Russian blue honeysuckle implied polygenetic inheritance of taste and aroma, selection of sweet tasting fruit requiring combination of 'sweetish-sour' and 'sweet' or 'sour' parents (Hayrova 1996). In the current study, polygenic inheritance is confirmed for both taste and aroma. Though additive gains may be difficult to achieve for either taste or aroma, high H^2 should make selection of more sweet and aromatic genotypes possible in any one generation. No specific combination of foundation groups can be recommended over another, confirming the initial observation of good flavours in all three foundation groups at the U of S (Bors 2009).

5.2.6.6 Fruit Mold and Firmness of Fruit Flesh

There was very little difference between the three improved groups for incidence or severity of fruit mold, each being mold free in 80-85% of harvests with the occasional rating reaching up to 'severe' (**Table 5.15; Appendix C.11**). Phenotypic averages for each improved group were intermediate to the high Kuril and low Russian group averages, being close to the intermediate Japanese group's average. Each improved group had genotypes that were always mold free, whereas the Japanese/Russian group had genotypes with the most frequent fruit mold observations compared to the other improved groups. H^2 was high to very high across the foundation and improved germplasm combined and separate and in each group on its own except for the Kuril and Kuril/Russian groups for which it was negligible and moderate, respectively. Low h^2 was found for the Japanese/Kuril group and it was negligible otherwise (**Table 5.16**).

For each improved group, flesh firmness ratings approximated a normal distribution and stretched across the spectrum from 'very firm' to 'watery'. All improved groups were most often rated as 'doughy' with large proportions of 'firm', 'doughy-soft' and 'soft' ratings as well. The Japanese/Russian and Kuril/Russian groups were slightly less skewed toward 'firm' ratings compared to the firmer Japanese/Kuril group. The range of observations for the Russian group was broader than for the Japanese or Kuril group, but the range for each improved group was greater still, which may be related to differences in populations size. Particularly, the Kuril/Russian group had the firmest and softest genotypes in the entire germplasm. H^2 was high

across the foundation and improved germplasm combined and separate and for each group on its own except the Russian group for which it was very high. Negligible h^2 was seen in all groups.

Despite indications of a relationship between incidence of fruit mold and later phenology in foundation germplasm (**Section 5.2.5.6**), the same relationship was not seen in the improved germplasm. Rather, highly quantitative control and the potential to successfully apply selection in improved populations were suggested, though additive gains will likely be elusive. For flesh firmness, greater average firmness in the Japanese/Kuril group was unexpected as the Russian group was heavily skewed toward firmer fruit, while the Japanese and Kuril groups were much softer on average. Interpretation of the foundation germplasm trial demonstrated that breeding for firmer fruit should employ crosses between Japanese and Kuril groups to continue to increase fruit size (**Section 5.2.5.6**), which complements findings that the Japanese/Kuril group had the largest average fruit size (**Section 5.2.2.2**) in addition to the firmest fruit as suggested here. Although making additive gains in fruit firmness were not indicated by these data, the opportunity to successfully employ selection should be similar across combinations of foundation groups.

5.2.6.7 Ease of Fruit Detachment, Stem Retention and Picking Scar Quality

All three improved groups contained strength of fruit attachment ratings from 'extremely loose' to 'extremely tight' with approximately normal distributions (**Table 5.15**; **Appendix C.11**). The most common ratings for the Japanese/Kuril and Japanese/Russian groups were 'moderate', while the Kuril/Russian group was split between 'moderate' and 'moderately tight'. Overall, the Japanese/Kuril group had some skew toward looser attachment and the Kuril/Russian group slightly toward tighter attachment, and the Japanese/Russian group was relatively intermediate. The averages were not widely different from what would be expected from their respective parent groups. The Japanese/Kuril group had a looser extreme than any of the other groups and a similarly tight extreme than the Japanese group. The Japanese/Russian group had a similar loose extreme to the Japanese group and a very tight extreme equal to that of the Russian group, making for the largest range in phenotypic averages. The Kuril/Russian group had a looser extreme than any foundation group but a tight extreme close to that of the Russian group. H^2 was high across the foundation and improved germplasm combined and separate and in each group except the Kuril and Japanese/Kuril groups for which it was negligible and moderate, respectively. Negligible h^2 was observed for all improved groups combined and separate (**Table 5.16**).

For harvest contamination with stems, the improved groups were intermediate to their respective foundation groups but tended to have a greater proportion of harvests completely free of stems with progressively fewer ratings for each successive degree of contamination. The Kuril/Russian group's average was slightly higher than for the other two improved groups. All three improved groups had genotypes that were consistently free of stems, which was not seen in any of the foundation groups. The most contaminated extreme in the Japanese/Kuril group was slightly less contaminated than the worst in its parent groups, while that of the Kuril/Russian and Japanese/Russian groups superseded the most contaminated extremes of their respective parent groups. H^2 was high to very high across the foundation and improved germplasm combined and separate and each group on its own except for the Kuril and Russian groups for which it was negligible. Low h^2 was seen across the improved germplasm and for the Japanese/Kuril and Japanese/Russian groups on their own, but it was negligible for the Kuril/Russian group.

The three improved groups had similar distributions in picking scar quality, with mostly 'small and dry' ratings, as for the Russian group. The Japanese/Kuril group had moderate proportions of 'small and wet' and 'large and dry' ratings. The Japanese/Russian group had a moderate proportion of 'large and dry' ratings. The Kuril/Russian group had moderate proportions of 'small and wet', 'large and dry' and 'large and wet' ratings. H^2 was high to very high across the foundation and improved germplasm combined and separate and in each group on its own without exception. Low h^2 was seen for the Japanese/Kuril and Japanese/Russian groups, and it was negligible for the Kuril/Russian group and across the improved germplasm.

Study of OP Russian populations suggested maternal effects in the inheritance of attachment strength as it relates to pre-harvest shattering and that there is a correlation between larger fruit and lower degrees of shattering (Hayrova 1996). The current study does not corroborate either of these suggestions but implies polygenic inheritance. Further, patterns between improved groups and comparisons with their foundation groups did not permit clear interpretation of a means of breeding for looser attachment. Similarly, the contamination of harvests with stems presented as a quantitative trait but perhaps with some dominance of lower degrees of contamination inherited from the Japanese group. The proportion of dry scars in the improved germplasm was proportional to those of their respective foundation groups, the Japanese and Russian groups combining to make the improved group with the highest proportion and the Kuril and Russian groups combining to make the improved group with the lowest proportion. The

same could not be said about small scar types because the Kuril and Russian groups had the highest combined proportions of small scars but made the improved group with the lowest proportion.

5.2.6.8 Selection Index

A relative SI calculated from these ratings (**Figure 5.10**; **Appendix C.12**) extended findings for the foundation germplasm (**Section 5.2.5.8**) to the improved germplasm. Overall, each improved group had a broader range in phenotypic scores compared to its respective parent group as expected due larger population sizes. The best score was in the Kuril/Russian group, followed by the Japanese/Kuril group and then the Japanese/Russian group. The worst score was also seen in the Kuril/Russian group, followed by the Japanese/Russian group and then the Japanese/Kuril group. Therefore, the broadest range in scores was seen in the Kuril/Russian group, whereas the range for the Japanese/Russian group was somewhat broader than for the Japanese/Kuril group, which had the smallest population size. The average score was only marginally better for the Japanese/Kuril group than the Japanese/Russian group, which was slightly better than for the Kuril/Russian group. There was no skew for any improved group.

The importance of positive and negative traits varied across improved groups (**Figure 5.11**). The Japanese/Kuril group most benefited, in order of importance, from closed distal ends, even fruit surfaces, loose fruit attachment, lack of stems retained in harvest, circular shape in cross-section, firm fruit flesh and good picking scar quality. Uniformity of fruit shape, complete synanthy, somewhat strong fruit aroma and sweeter fruit tastes were positive traits of less importance. Negative traits were confined to light fruit colour, prevalence of pubescence and weak bloom. The Japanese/Russian group most benefited from circular shape in cross-section, lack of stems retained in harvest, loose fruit attachment, good picking scar quality and strong fruit aroma. Sweet fruit taste, lack of pubescence and a somewhat heavy bloom were less important as positive traits. Light fruit colour was the most important negative trait, followed by soft fruit flesh, prevalence of incomplete synanthy, heterogeneity in fruit size and shape, open distal ends, prevalence of fruit mold and uneven fruit surfaces. The Kuril/Russian group was positively affected by dark fruit colour, complete synanthy, heavy bloom, uniform fruit shape, lack of pubescence and low incidence of mold. Negative traits included narrow shape in cross-section, large distal end openings, soft fruit flesh, tight attachment to the plant, retention of stems in harvest and poor picking scar quality followed by uneven fruit surfaces, weak aroma and sour taste.

199
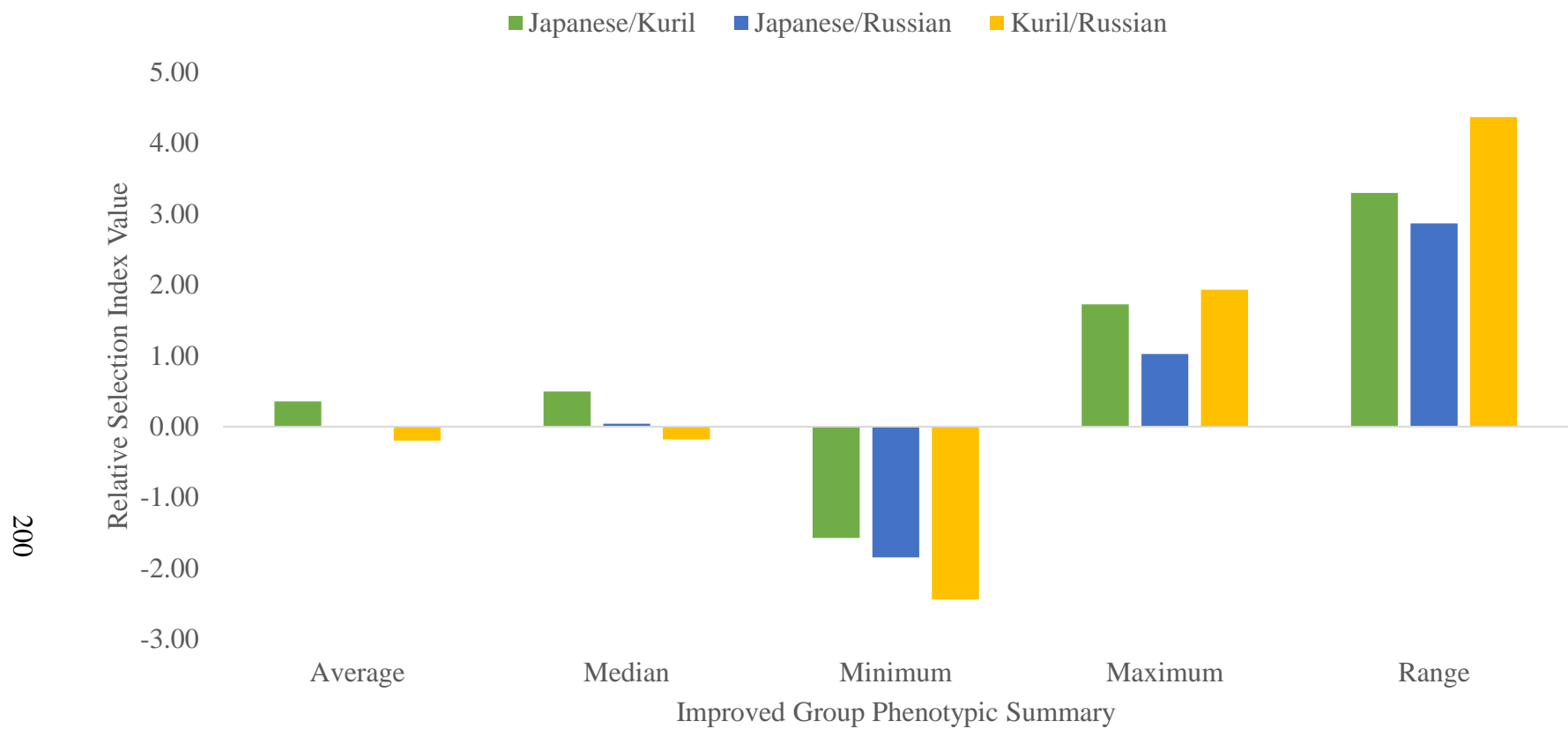
Figure 5.10. Improved Germplasm: Phenotypic summary of relative selection index for 16 fruit agronomic ratings for blue honeysuckle in 2012/2013 in Chilliwack, BC, Canada.
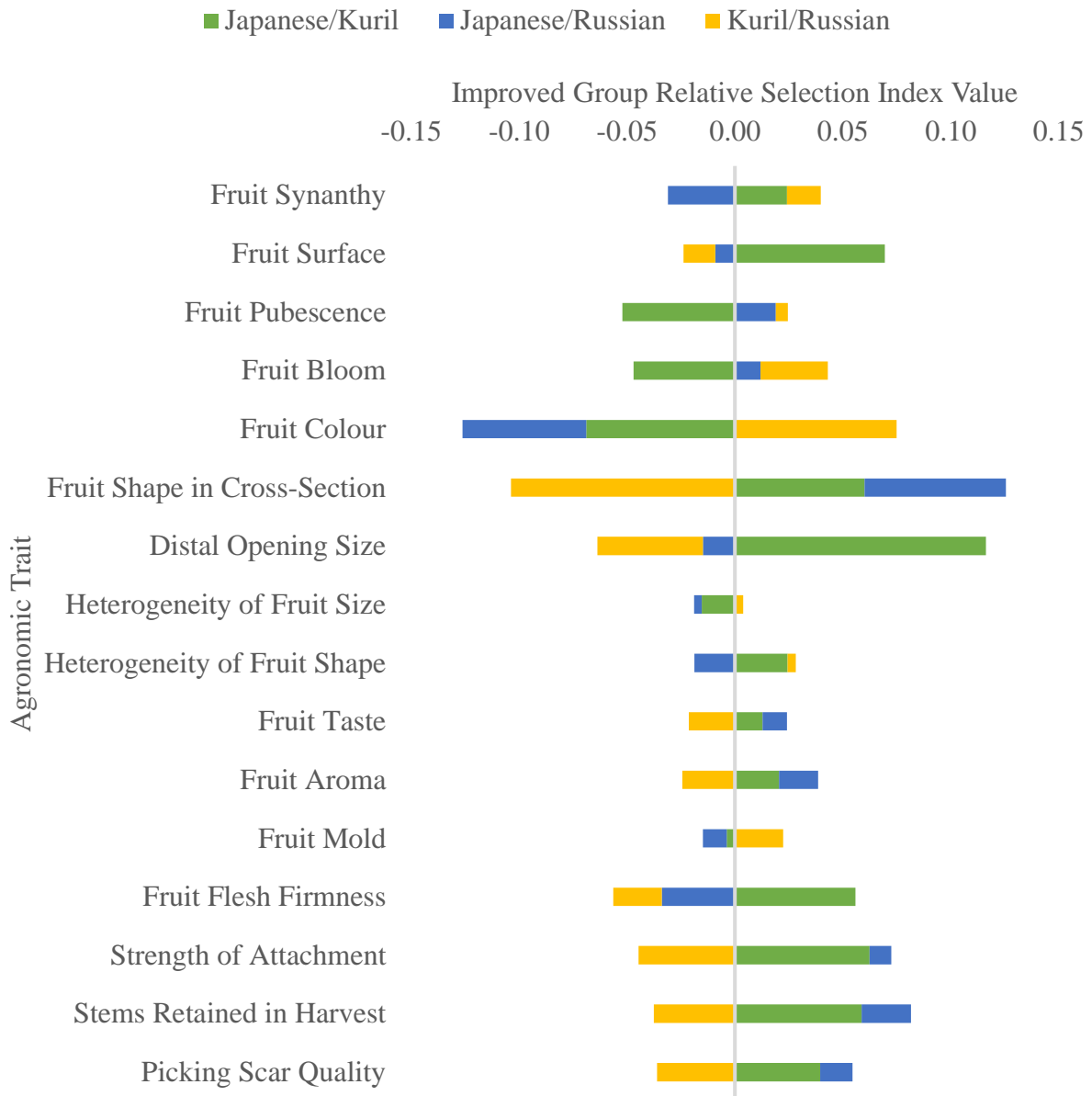
Figure 5.11. Improved Germplasm: Effects of 16 fruit agronomic ratings on a relative selection index for blue honeysuckle in 2012/2013 in the Chilliwack, BC, Canada.

6. CHAPTER 6: BIOCHEMICAL TRAITS RELATED TO FRUIT QUALITY AND POTENTIAL HUMAN HEALTH BENEFITS IN BLUE HONEYSUCKLE GERMPLASM

6.1 Introduction

As a complex trait, fruit quality (FQ) has many inter-related components that impact marketability. Blue honeysuckle flavours are highly variable, but most cultivars are relatively tart due to a low total soluble solids to titratable acidity ratio (TSS:TA) (Thompson 2006a). This is an important limitation to mainstream appeal for fresh consumption, and genetic enhancement through breeding is essential to expansion of the crop's marketing potential (Thompson 2006b). This limitation is counter-balanced by the crop's traditional use as a therapeutic and prophylactic medicine due to the potential human health benefits related to its nutritional content (Makarov et al 2009). As an important motivation for its development, scientific and popular interest in blue honeysuckle are based on its high levels of vitamins, minerals and plant secondary metabolites (Bakowska-Barczak et al 2007). Particularly, blue honeysuckle fruit are very high in polyphenolics, which relates to high antioxidant activity (AOA) (Palíková et al 2008). Evaluating FQ and nutritional content across blue honeysuckle germplasm in a temperate climate requires direct comparison with other large-scale commercial fruit crops to understand future opportunities for crop development and marketability. Knowledge gaps include actual quantification of FQ and nutritional content in foundation germplasm groups, elucidation of the opportunities for crop enhancement using improved germplasm groups and description of the physiological and genetic complexity underpinning these important fruit biochemical traits. To address these research questions, FQ and nutritional content were evaluated in a range of blue honeysuckle germplasm in a temperate climate in the Fraser Valley, British Columbia, Canada.

6.2 Results and Discussion

6.2.1 Fruit Quality in Foundation Germplasm

6.2.1.1 Description and Comparison of Foundation Germplasm Groups

On average, dry matter (DM) was higher for the Japanese (15.3%) and Russian groups (15.2%) than the Kuril group (14.2%) (**Figure 6.1**; **Table 6.1**). TSS was higher for the Japanese group (11.5%) than the Kuril (10.4%) and Russian groups (10.3%). TA was higher for the Japanese group (2.65%), considerably lower for the Kuril group (2.26%) and even lower for the
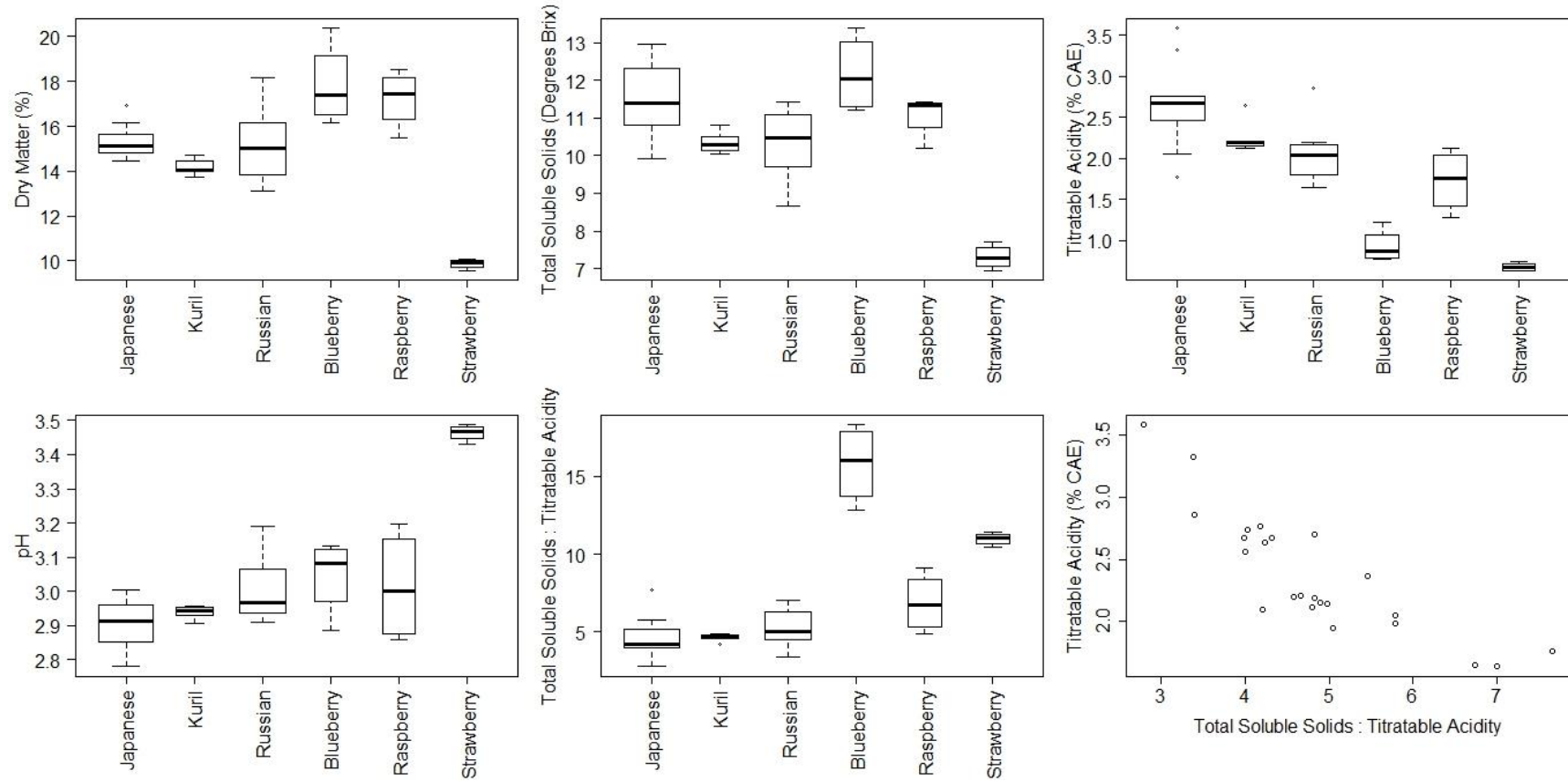
Figure 6.1. Foundation Germplasm: Fruit quality traits in blue honeysuckle and comparison crops in 2012/2013 in the Fraser Valley, BC, Canada and XY plot of two key fruit quality traits (CAE – citric acid equivalents, boxplot widths are proportional to the square root of the sample size for each group)

Table 6.1. Foundation Germplasm: Biochemical determinations of fruit quality in blue honeysuckle and comparison crops in 2012/2013 in the Fraser Valley, BC, Canada.

		Japanese	Kuril	Russian	Blueberry	Raspberry	Strawberry
Dry Matter (%)	Average	15.3	14.2	15.2	17.8	17.2	9.9
	Median	15.1	14.0	15.0	17.4	17.5	9.9
	Minimum	14.5	13.7	13.1	16.2	15.5	9.6
	Maximum	16.9	14.7	18.2	20.4	18.5	10.0
	Range	2.5	1.0	5.1	4.2	3.0	0.5
Total Soluble Solids (%)	Average	11.5	10.4	10.3	12.2	11.1	7.3
	Median	11.4	10.3	10.5	12.0	11.3	7.3
	Minimum	9.9	10.1	8.7	11.2	10.2	7.0
	Maximum	13.0	10.8	11.4	13.4	11.4	7.7
	Range	3.0	0.8	2.8	2.2	1.2	0.8
Titratable Acidity (% Citric Acid Equivalents)	Average	2.7	2.3	2.1	0.9	1.7	0.7
	Median	2.7	2.2	2.0	0.9	1.8	0.7
	Minimum	1.8	2.1	1.6	0.8	1.3	0.6
	Maximum	3.6	2.6	2.9	1.2	2.1	0.7
	Range	1.8	0.5	1.2	0.5	0.8	0.1
pH	Average	2.90	2.94	3.00	3.05	3.01	3.46
	Median	2.91	2.94	2.97	3.08	3.00	3.47
	Minimum	2.78	2.91	2.91	2.89	2.86	3.43
	Maximum	3.00	2.96	3.19	3.13	3.20	3.49
	Range	0.22	0.05	0.28	0.25	0.34	0.06
Total Soluble Solids:Titratable Acidity	Average	4.6	4.6	5.2	15.8	6.9	11.0
	Median	4.2	4.7	5.0	16.0	6.7	11.0
	Minimum	2.8	4.2	3.4	12.8	4.8	10.5
	Maximum	7.7	4.9	7.0	18.3	9.1	11.4
	Range	4.9	0.7	3.6	5.5	4.3	0.9

Russian group (2.06%). Variation between foundation groups was less distinct for pH, with averages of 2.90, 2.94 and 3.00 for the Japanese, Kuril and Russian groups, respectively. TSS:TA was highest for the Russian group (5.24), followed by the Kuril (4.63) and then the Japanese group (4.58). The absolute ranges in TSS, TA and pH were similarly broader for the Japanese and Russian groups, whereas variation in DM was greater in the Russian than the Japanese group and the opposite was true for TSS:TA. The Kuril range was much more restricted for all determinations.

The Russian group had the absolute lowest DM, at 13.1% (R-2-14), as well as the absolute highest, at 18.2% (R-2-16), for a range of 5.1% (**Appendix D.1**). R-2-11 and R-2-06 also had quite low DM, whereas R-2-14 and R-27-35 were higher and R-2-07 and R-2-10 were intermediate. J-66-53 had the highest (16.9%) and J-22-14 the lowest (14.5%) TSS in the Japanese group, which had a range that was half as wide as for the Russian group. The range in DM for the Kuril group spanned only 1%, and K-97-12 had the highest DM (14.7%), but it was not statistically different from the others. Therefore, the Japanese and Russian groups had higher average DM compared to the Kuril group. Both the highest and lowest DM were observed in the Russian group, but the lowest in the Japanese group barely overlapped with the highest in the Kuril group. The Russian group overlapped both the Japanese and Kuril groups, while the Japanese ranged from equivalent with the highest Kuril to 3.5% higher.

The absolute range for TSS was highest for the Japanese group, spanning approximately 3% from the lowest extreme, at 9.9% (J-444-39), to the highest, at 12.8% (J-21-78, J-46-55 and J-66-53). Only J-73-39 had as low a TSS as J-444-39, though neither of these had lower TSS than the four late Kuril genotypes (**Section 4.2.1.1**) or the lower range of the Russian group. K-97-12 (10.8%) had significantly higher TSS than only J-444-39 in the Japanese group. There were no statistical differences between Kuril genotypes, which had a narrow TSS range of 0.8%. Within the Russian group, R-2-14 had the lowest TSS (8.7%), which was lower than all other genotypes except for R-2-06 (9.7%). R-2-06, R-2-07, R-2-10 and R-2-11 had similar TSS to the Kuril group and some of the lower Japanese genotypes. R-2-16 (11.2%) and R-27-35 (11.4%) had the highest TSS in the Russian group but were equivalent to average Japanese genotypes as well as K-97-12.

The absolute range in TA was also highest for the Japanese group (1.82%) followed by the Russian (1.22%) and then the Kuril group (0.52%). J-444-39 had the absolute highest TA (3.58%) and R-2-07 and R-2-16 the absolute lowest (1.65%) (**Appendix D.2**). The narrow absolute range

for the Kuril group was overlapped by the highest and lowest genotypes in the Japanese and Russian groups, respectively. Within the Japanese group, J-46-55 had the lowest TA (1.76%), which was lower than for any other Japanese and Kuril genotypes and all but three Russian genotypes. J-45-14 and J-21-78 also had low TA and were like the four late Kuril genotypes and the intermediate Russian genotypes. There were six intermediate Japanese genotypes, but J-22-14 and J-444-39 had statistically higher TA than any other blue honeysuckle or comparison crop genotype (**Section 6.2.1.2**). Further, J-444-39 was statistically higher than even J-22-14. Within the Kuril group, the four late genotypes were statistically equivalent (2.11-2.21%), but K-97-12 was significantly higher (2.64%). This was similar to the six intermediate Japanese genotypes and higher than all Russian genotypes except R-2-13 (2.86%). Within the Russian group, R-2-07 and R-2-16 had lower TA than any other Russian or Kuril genotype and all but the lowest Japanese genotype, J-46-55. Aside from R-2-13, the other five Russian genotypes were statistically equivalent to one another, in the same range as the late Kuril genotypes and statistically lower than the six intermediate Japanese genotypes.

In summary, the Japanese group had higher average TSS than the Kuril and Russian groups, which had similarly low averages. The Japanese group also had higher average TA than the Russian group, but the Kuril group was relatively intermediate. For TSS, absolute range was only slightly broader for the Japanese than the Russian group and was several times broader than for the Kuril group. Correspondingly, the range in TA was broader in the Japanese group, followed by the Russian group, whereas the Kuril group's range was much narrower. Consequently, the genotypes with the highest and lowest TSS and TA were found in the Japanese and Russian groups, respectively, both groups completely overlapping the Kuril group.

The absolute pH ranges in the Japanese and Russian groups were 0.22 and 0.28, respectively, but the range in the Kuril group was a mere 0.05. The Japanese group had the lowest extreme and the Russian group the highest, the extremes of both groups overlapping the entire range of the Kuril group. Within the Japanese group, J-444-39 had the lowest pH (2.78), which was significantly lower than all but J-22-14 (2.84). J-46-55 (3.00) had the highest pH, but was the same as J-21-78 (2.98) and J-45-14 (2.99), whereas all other genotypes were intermediate within a narrow range. There were no significant differences between the Kuril genotypes, and the lowest, K-3-07 (2.91), was statistically higher than only J-444-39 in the Japanese group. In contrast, the highest, K-97-12 (2.96), was equivalent to all Russian genotypes except for R-2-07, R-2-16 and

R-27-35 (3.19, 3.08 and 3.05, respectively), which had the highest pH in the foundation germplasm. R-2-06, R-2-10, R-2-11 and R-2-14 had significantly lower pH at 2.95, 2.94, 2.91 and 2.94, respectively.

As pH is measured on a logarithmic scale, variation across the foundation germplasm was numerically quite small, ranging from 2.90 in the Japanese group to 3.20 in the Russian group. This range contrasted with the trend for TA, which is expected for these negatively correlated traits. The absolute range in the Japanese group, in contrast to TA, was slightly more restricted than for the Russian group but still more than four times broader than for the Kuril group. The lowest and highest pH were discovered in the Japanese and Russian groups, respectively, and both groups completely overlapped the range of the intermediate Kuril group. There was significant overlap between all foundation groups and fewer statistical differences between genotypes than for the other FQ traits.

Absolute range in TSS:TA was broadest for the Japanese group (4.88), slightly narrower for the Russian group (3.60) and much more restricted for the Kuril group (0.66). Therefore, the Japanese group had both the highest and lowest TSS:TA, but both the Russian and Japanese groups completely overlapped the Kuril group. Within the Japanese group, J-444-39 had the lowest TSS:TA (2.78), followed by J-22-14 (3.37). J-46-55 had the highest TSS:TA (7.66), which was significantly higher than for any other Japanese genotype though there were two Russian genotypes with equivalent TSS:TA. J-45-14 (5.79) and J-21-78 (5.46) also had high ratios, while the remaining genotypes were statistical intermediates. Within the Kuril group, K-97-12 had the lowest ratio (4.23) but was not significantly different from any of the late Kuril genotypes, which were not different from one another. There were few statistical differences between Kuril genotypes and the low to intermediate Japanese genotypes, but there were only two Russian genotypes that had statistically higher ratios than the Kuril genotypes. There were no statistical differences between Russian genotypes, but R-27-35 (5.79) had a higher ratio than the lowest Japanese genotype, while R-2-07 (6.73) and R-2-16 (6.99) had higher ratios than all Kuril genotypes and all but the three highest Japanese ratios.

The pattern in TSS:TA contrasted with TA but was similar to pH. Comparison to TSS was more complex. As for TA, the Japanese group had a considerably broader absolute range compared to the Russian group, whereas the Kuril group had a very narrow range. This resulted in the Japanese group having the highest and lowest ratios, while both the Japanese and Russian

groups overlapped the intermediate Kuril group. The Japanese group's broader absolute range for TSS and TA resulted in complete overlap of both the Kuril and Russian groups for TSS:TA. The narrow range of TSS:TA for the Kuril group was due to limited variation in both TSS and TA. The differences in TSS:TA across the foundation germplasm more directly reflected the differences in TA than in TSS (**Section 6.2.1.4**). The low average Japanese TSS:TA coincided with both higher TSS and TA. Contrastingly, high average Russian TSS:TA was seen with both lower TSS and TA. Intermediate Kuril TSS:TA was associated with moderate TA and with TSS that was nearly as low as for the Russian group. Therefore, the Japanese group had a low average ratio despite having high TSS, and the Russian group had a high average ratio despite having low TSS.

To date, there are no reports to compare DM in either the Japanese or Kuril groups. However, considerably lower DM was observed for Russian germplasm in several cold continental climates in Russia and several Eastern European countries (**Table 6.2**) (Plekhanova 2000; Golovunin 2009; Prischepina 2000; Petrushua 2009; Ochmian et al 2008; Rupasova et al 2009). Compared to the Fraser Valley, higher DM was observed in warmer, though still continental, climatic regions of Poland (Poznan), Lithuania (Vilnius) and Slovakia (Nitra) (Chmiel et al 2014; Žilinskaitė et al 2007; Juríková et al 2014). In summary of the literature, Russian germplasm has 1) consistently lower DM in the coldest continental climates compared to the temperate climate of the Fraser Valley; 2) DM as high as in the Fraser Valley in less severe continental climates; and 3) more variability in DM than observed in the current study. The underlying cause of lower DM in colder climates cannot be validated from the limited data available. Speculatively, the Russian germplasm's poor fruit set in temperate climates (**Section 5.2.1.4**) is related to its extremely early phenology (**Section 4.2.1.1**), which may inhibit full fruit sizing during later stages of development and result in higher DM.

As for DM, no literature reports of TSS, TA, pH or TSS:TA are available for the Kuril group. However, reports of TSS from Japan tended to be slightly higher across a broad range of selections (Takada et al 2003), but 'Yufutsu' was reported to have slightly lower TSS (Tanaka et al 1994) than the average described in the current study. A much broader sampling of selections in Oregon showed a nearly identical range for TSS (Thompson and Barney 2007), which was expected as this was the source for the Japanese germplasm used in the current study, both regions have temperate climates and optimal ripeness was evaluated based on phenology (**Section 4.2.1.1**).

Table 6.2. Biochemical determinations of fruit quality in blue honeysuckle (KGCC – Köppen-Geiger Climate Classification, DM – dry matter, TSS – total soluble solids, TA – titratable acidity, CAE – citric acid equivalents).

Location	KGCC	DM (%)	TSS (%)	TA (% CAE)	pH	TSS:TA	Reference
Japan (Hokkaido)	*Dfa*		10.3-17.0		2.58-3.29		Takada et al 2003
Japan (Hokkaido)	*Dfa*		10.5	2.17			Tanaka et al 1994
Japan (Hokkaido)	*Dfa*			2.92	2.77		Tanaka and Tanaka 1998
USA (Corvallis)	*Csb*		9.7-13.0	1.91-4.86	2.42-3.57	1.57-5.93	Thompson and Barney 2007
Russia (Pavlovsk)	*Dfa*	10.3-16.6					Plekhanova 2000
Russia (Mari El Republic)	*Dfb*	12.9-16.4	6.6-9.5	2.50-3.60			Goluvunin 2009
Russia (Altai krai)	*Dfa*	12.2-14.8	8.2-9.7	3.33-4.48			Prischepina 2000
Russia (Kamchatka krai)	*Dfc*	11.7-12.5	7.2-9.2	2.00-2.90		2.59-4.05	Petrushua 2009
Russia (Southern Urals)	*Dfb*		11.1-13.1				Murslimova 2013
Russia (Tomskaya oblast)	*Dfc*		6.6-9.8				Suchkova and Senina 2009
Poland (Rajkowo)	*Dfb*	11.6-14.7	11.6-12.1	2.82-3.61		2.60-9.70	Ochmian et al 2008
Poland (Krakow)	*Dfb*		10.3-11.6	2.60-3.10			Malodobry et al 2010
Poland (Skierniewice)	*Dfb*		10.1-15.8	1.43-2.14	3.00-3.55	4.81-9.49	Wojdyło et al 2013
Poland (various)	*Dfb*	11.4-18.5					Chmiel et al 2014
Belarus (Minsk)	*Dfb*	11.9-14.7					Rupasova et al 2009
Lithuania (Vilnius)	*Dfb*	12.2-21.0					Žilinskaitė et al 2007
Slovakia (Nitra)	*Dfb*	14.2-18.2	3.3-9.5	1.52-2.62			Juríková et al 2014a
Ukraine (Krasnokutsky)	*Dfb*		5.9-9.0	1.82-2.72			Grizodub 2009
Romania (Pitesti)	*Dfb*		13.0-17.2				Ancu et al 2011
Canada (Saskatchewan)	*Dfb*		18.2-22.9		3.10-3.34		Bors et al 2012

Report of TA from Japan (Tanaka and Tanaka 1998) showed similarity to the average found in the current study, but no comparison of the genetic range is possible from the limited data provided. In Oregon, TA did not range quite as low as in the Fraser Valley, but it had a considerably higher upper extreme, greater overall range and higher average across a greater number of genotypes (Thompson and Barney 2007). For pH, reports from Japan (Takada et al 2003; Tanaka and Tanaka 1998) and Oregon (Thompson and Barney 2007) compared equally to the Fraser Valley, having much broader ranges and very similar averages.

No reports of TSS:TA are available from Japan, but there was a slightly narrower range of generally lower values in Oregon (Thompson and Barney 2007). Since the range for TSS was very similar between Oregon and the Fraser Valley, this lower range in TSS:TA is clearly related to the observation of higher TA (**Section 6.2.1.4**) in the unselected material in Oregon. This is compared to the genotypes that were selected from this same material based primarily on taste, which apparently shifted the germplasm in the current study toward lower TA but not higher TSS.

Compared with the current study, evaluation of Russian material in Russia showed TSS from slightly higher, in the southern Urals (Murslimova 2013), to mostly lower values across several regions (Prischepina 2000; Petrushua 2009; Plekhanova 2000; Golovunin 2009; Suchkova and Senina 2009). Compared with other blue honeysuckle taxa, ssp. *kamtschatica* and *edulis* stand out for relatively high TSS:TA (Plekhanova 2000). The lower TSS:TA ratios in several of these studies are explained by the inclusion of taxa other than ssp. *kamtschatica* and *edulis*, whereas the current study was restricted to these taxa. Also, Polish (Ochmian et al 2008; Malodobry et al 2010; Wojdyło et al 2013) and Romanian (Ancu et al 2011) studies showed much higher TSS:TA ratios, while a Slovakian study (Juríková et al 2014) demonstrated lower ratios but a broad range.

In contrast, TSS was far higher in Saskatchewan (Bors et al 2012) than in the Fraser Valley, which is likely because the fruit were left to ripen on the plant longer after fruit colouring (**Section 4.2.1.1**) than in the current study, which also explains the higher pH values for the latter. Also, cooler night-time temperatures in Saskatchewan result in lower metabolic rates and greater accumulation of sugars. For TA, all but one report from Russia (Petrushua 2009) and another from Poland (Wojdyło et al 2013) present higher values than in the current study, some by two percent or more. Also, a report from the less severe continental climate of Ukraine's Krasnokutsky district (Grizodub 2009) showed a nearly identical TA range to the Fraser Valley. Compared to the Fraser Valley, TSS:TA was lower in the extremely cold climate of the Kamchatka krai (Petrushua 2009),

higher in central Poland (Wojdyło et al 2013) and ranged from lower to higher in a less severe continental climate in northwestern Poland (Ochmian et al 2008).

Therefore, though TSS is typically lower in continental climates, TA is typically much higher, which likely relates to major difference between methods used to determine harvest date. In most Eurasian studies (e.g., Gawroński et al 2014; Murslimova 2013; Korobkova 2009), multiple harvests from each plant are used to avoid loss of fruit to pre-harvest shattering, but a single, simultaneous harvest of each plant was possible in the Fraser Valley as in Oregon. Therefore, the fruit sampled in Russia and eastern Europe had likely not reached optimal ripeness compared to the fruit collected in the current study. This explains the lower TSS and higher TA, despite the more moderate climatic conditions during development, which likely would have the opposite effect if methods were equivalent. Namely, hotter, drier conditions cause higher TSS and lower TA than cool, rainy weather in Pavlovsk (Plekhanova 1989) and the southern Urals (Murslimova 2013). A mild winter in the Fraser Valley results in an earlier start to the season than in continental climates (**Section 4.2.1.1**), which tend to warm up quicker once they do begin, resulting in a more compact season with cooler night time temperatures. The important impact of differences in methods on determinations of FQ is supported by analyses of sequential harvests of blue honeysuckle in Poland (Ochmian et al 2013) and in Russia's Tambov oblast (Belosohov and Belosohova 2011) where DM, TSS and TSS:TA increased while TA decreased over the season.

6.2.1.2 Blueberry, Raspberry and Strawberry Compared to Foundation Germplasm

Direct comparison of blue honeysuckle FQ to other crops is available for only Russian germplasm. DM of 14% was lower than for black mulberry (*Ribes nigrum* L.), bilberry (*Vaccinium myrtillus* L.), European juneberry (*Amelanchier ovalis* Medik.) and blackberry (*Rubus plicatus* Weihe & Nees) in Poland (Zadernowski et al 2005). Also, in the Czech Republic, DM of 13.84-18.11% was higher and TA of 1.46-2.94% was intermediate to Saskatoon berry (*Amelanchier alnifolia* Nutt.), black mulberry (*Morus nigra* L.), Nanking cherry (*Prunus tomentose* Thunb.) and jostaberry (*Ribes* ˣ*nidigrolaria* Rud. Bauer & A. Bauer) (Juríková et al 2012b). As these comparisons of DM and TA were against other niche crops with their own FQ concerns, they did not evaluate the large-scale commercial potential for blue honeysuckle. Therefore, the current study is the first biologically replicated experimental evaluation of FQ in a range of blue honeysuckle germplasm with direct comparisons to large-scale commercial crops.

211

For DM, blueberry had a broad range (16.2-20.4%) from equivalent to the higher Japanese and Russian genotypes to significantly higher than any blue honeysuckle genotype (**Figure 6.1**; **Table 6.1**; **Appendix D.1**). Raspberry DM varied by 3% (15.5-18.5%), each cultivar being equivalent to one or more of the highest DM genotypes in the blue honeysuckle germplasm. With a range of less than 0.5%, there were no differences between strawberry cultivars, which all had significantly lower DM than any other crop.

With an overall range in TSS of 2.2%, the lowest blueberry cultivars, 'Duke' (11.2%) and 'Reka' (11.4%), were not significantly higher than most the Russian group, intermediate Japanese genotypes or K-97-12, but they were lower than the three highest Japanese genotypes. The higher TSS cultivars, 'Bluecrop' and 'Elliott' (12.7 and 13.4%, respectively), were significantly higher than all but the three highest Japanese genotypes. The absolute ranges in TSS for raspberry and strawberry were low (1.2 and 0.8%). The higher TSS raspberry cultivars, 'Chemainus' (11.3%), 'Saanich' (11.4%) and 'Meeker' (11.4%), were statistically higher than all Kuril genotypes, except K-97-12, equivalent to the higher Russian and intermediate Japanese genotypes and lower than the three highest Japanese genotypes. The lower TSS raspberry cultivar, 'Cascade Bounty' (10.2%), was equivalent to the intermediate Russian, all Kuril and most Japanese genotypes though lower than several of the higher Japanese genotypes. Strawberry TSS was very low and only the highest cultivar, 'Totem' (7.7%), was equivalent to any other crop genotype (*viz.* R-2-14).

Blueberry TA ranged 0.45% from 'Reka' (0.77%) to 'Elliott' (1.22%), all being significantly lower than even the lowest blue honeysuckle (**Appendix D.2**). Average raspberry TA was lower than the average for each blue honeysuckle foundation group, ranging 0.84% from 'Saanich' (1.28%) to 'Cascade Bounty' (2.12%). The higher end of this range was equal to the intermediate Russian, four late Kuril lower Japanese genotypes. However, the lower end was significantly lower than all blue honeysuckle genotypes. Variability in TA for strawberry was very low, ranging 0.11%, and there were no statistically significant differences between cultivars, which all had far lower TA than any blue honeysuckle genotype.

With a moderate degree of variation, blueberry pH ranged 0.25 from 'Elliott' (2.89) to 'Reka' (3.13). The bottom end of this range was lower than the highest Japanese and Russian genotypes, higher than the lowest blue honeysuckle genotype (J-444-39) and equivalent to most of the Kuril group. 'Reka' was higher than most of the Japanese, all the Kuril and all but the three highest Russian genotypes. Raspberry pH ranged from 'Cascade Bounty' (2.86) to 'Saanich'

(3.20). The former only measured higher than J-444-39 and was equivalent to most of the rest of the blue honeysuckle germplasm, whereas the latter was equivalent to the highest blue honeysuckle genotype (R-2-07). With a very narrow absolute range (0.06), there were no statistical differences between strawberry cultivars, but all had significantly higher pH than any other genotype of any other crop.

For blueberry, 'Elliott' had the lowest TSS:TA (12.81) and 'Bluecrop' the highest (18.33). These ratios were mostly higher than for raspberry and strawberry. Raspberry ratios ranged from 'Cascade Bounty' (4.85) to 'Saanich' (9.12). 'Cascade Bounty' was similar to the intermediate blue honeysuckle genotypes in each foundation group and surpassed only the very lowest genotype (J-444-39). 'Saanich' was equal to the highest Japanese and Russian genotypes. All four strawberry cultivars had significantly higher ratios than even the highest ratio in blue honeysuckle germplasm, but there were no statistical differences between strawberry cultivars. As intermediate to the blueberry and raspberry cultivars, 'Rainier' (11.19) and 'Stolo' (11.39) were equivalent to the lowest ratio blueberry cultivar ('Elliott'), while 'Puget Reliance' (10.83) and 'Totem' (10.45) were equivalent to the highest ratio raspberry cultivar ('Saanich').

Compared with literature (**Table 6.3**) the current findings were within the same general ranges. As expected, variations were observed across studies due to different locations, years and experimental methods. In summary, blueberry had the highest average DM (17.8%), whereas the averages for raspberry and strawberry (17.2 and 9.9%) were higher and lower than for blue honeysuckle, respectively. Similarly, blueberry had the highest average TSS (12.2%) with raspberry approximately a percent lower (11.1%), which was slightly lower than the Japanese group's average, higher than the Kuril and Russian group averages and much higher than the strawberry average (7.3%). In contrast, blueberry had a lower average TA (0.93%) than any blue honeysuckle foundation group, while raspberry and strawberry had higher (1.73%) and lower (0.67%) averages, respectively. The average pH for raspberry (3.01) and blueberry (3.05) were similar to the blue honeysuckle foundation groups, but the strawberry average was considerably higher (3.46). Average blueberry TSS:TA was far higher (15.79) than any blue honeysuckle foundation genotype and had a wide absolute range (5.52). The average raspberry ratio (6.86) overlapped with the upper range of the blue honeysuckle foundation groups and had a broader range (4.28) as for blueberry. Strawberry ratios were more intermediate (10.97) and had a small absolute range (0.93).

Table 6.3. Biochemical determinations of fruit quality in blueberry, raspberry and strawberry comparison crops in literature from the Pacific Northwest (TSS – total soluble solids, TA – titratable acidity, CAE – citric acid equivalents).

Crop	Cultivar	TSS (%)	TA (% CAE)	pH	TSS:TA	References
Blueberry	'Bluecrop'	11.5	0.46	3.10	24.9	Saftner et al 2008; Kim et al 2013
	'Duke'	10.8	0.43	3.00	25.5	
	'Elliott'	10.7	1.60	3.40	9.0	
	'Reka'	11.3	1.22	2.50	9.2	
Raspberry	'Cascade Bounty'	10.6	1.26	2.39	8.4	Moore 2007; Kempler et al 2006; Kempler et al 2008
	'Chemainus'	10.4	1.24	2.89	8.3	
	'Meeker'	12.1	0.85	2.70	14.2	
	'Saanich'	10.3	1.24	3.10	8.3	
Strawberry	'Puget Reliance'	7.8	0.70	3.27	11.1	Moore et al 1995; Shamaila et al 1992; Kempler et al 2011
	'Rainier'	7.6	1.07	3.32	7.1	
	'Stolo'	8.7	0.90	3.52	9.7	
	'Totem'	8.4	1.07	3.35	7.9	

6.2.1.3 Out-group Comparisons to Foundation Germplasm

The Japanese out-group comparison genotype, J-PP, was statistically the same as most of the Japanese foundation group for DM (15.1%), pH (2.99) and TSS:TA (5.10) and as both the Japanese and Russian groups for TSS (10.8%) (**Appendix D.1**; **Appendix D.2**). In contrast, it had equivalent TA to the second lowest Japanese genotype (J-45-15).

'Borealis' had the lowest DM (12.6%) of any blue honeysuckle genotype, which was equivalent to only R-2-14 and R-2-06; very low TSS (8.7%) that was equivalent to only R-2-14 but still significantly greater than for any strawberry cultivar; high TA (2.95%) that was statistically higher than any Kuril or Russian genotype and significantly lower than only J-22-14 and J-444-39 in the Japanese group; low pH, which was only higher than J-444-39 but lower than J-46-55 and the three highest Russian genotypes; and very low TSS:TA (2.96) that was equal to the lowest ratios in the foundation germplasm, including K-97-12. 'Tundra' had significantly higher DM (14.9%) and TSS (10.2%) than 'Borealis'. Therefore, for TSS, 'Borealis' was equivalent to K-97-12 and many Japanese and Russian genotypes for DM and equivalent to 'Cascade Bounty', most of the intermediate Japanese and Russian genotypes and the entire Kuril group. Similarly, 'Indigo Gem' had significantly higher DM (17.0%) and TSS (12.4%), which was equivalent to the highest Japanese genotype and R-2-13. 'Tundra' and 'Indigo Gem' had lower TA than 'Borealis', but were equivalent to one another, J-21-78 and the four late Kuril and intermediate Russian genotypes. Correspondingly, for pH, 'Tundra' and 'Indigo Gem' were not different from one another but were higher than 'Borealis', equivalent to most of the intermediate to high Japanese and Kuril genotypes and surpassed by only R-2-07 in the Russian group. 'Indigo Gem' (5.54) had significantly higher TSS:TA than 'Borealis' (2.96) but not 'Tundra' (4.92). The ratios for 'Borealis' and 'Tundra' were close to the highest ratios in each foundation group, but neither was significantly higher than K-97-12.

In Saskatchewan, 'Borealis' had TSS of 11.4%, TA of 2.42% and pH of 3.39, and 'Tundra' had TSS of 17.4% and TA of 1.42% (Bors et al 2012). TSS was much higher and TA much lower in Saskatchewan than in the Fraser Valley due to different experimental methods (**Section 6.2.1.1**), but relative differences were consistent. Further, 'Borealis' is described as "sweet tart", 'Tundra' as "sweet tangy" and 'Indigo Gem' as "sweet chewy" (Bors et al 2012). These subjective descriptions are validated by the current findings, 'Borealis' having the highest TA of the three, 'Tundra' the lowest TA and 'Indigo Gem' the highest DM.

6.2.1.4 Correlations Between Fruit Quality Traits

DM had a high positive correlation with TSS for all crops combined, the foundation germplasm combined and for the Japanese group and blueberry and strawberry cultivars on their own (**Table 6.4**). This positive correlation was moderate for the Kuril and Russian groups and raspberry cultivars on their own. Similarly, a moderate positive correlation between DM and TSS was seen in 106 Russian seedlings across ten populations (Hayrova 1996).

Negative correlations between DM and TA were low and moderate for the Russian group and raspberry cultivars, respectively. The only correlations between DM and pH were a low negative correlation across all crops, a moderate negative correlation for the Kuril group and a moderate positive correlation for the raspberry cultivars. While there was no general correlation of DM with TSS:TA across all four crops combined, there was a low positive correlation across the foundation germplasm and in the Japanese and Kuril groups on their own but not the Russian group. This relationship was moderate for the blueberry, raspberry and strawberry cultivars.

There was no general correlation between TSS and TA across all four crops or the foundation germplasm, but there was a low negative correlation for the Japanese group and raspberry cultivars on their own and a low positive correlation for the strawberry cultivars. A similar moderate negative correlation was observed in Russian seedling populations (Hayrova 1996). In contrast, there was a low negative correlation between TSS and pH across the foundation germplasm and for the Kuril group on its own. TSS had a moderate positive correlation with TSS:TA across the foundation germplasm and for the Kuril and Russian groups and raspberry and strawberry cultivars on their own but a high for the Japanese group.

There was a moderate negative correlation between TA and pH across the foundation germplasm and for the Japanese group on its own. This correlation was low for the Russian group and strawberry cultivars, high for the blueberry and raspberry cultivars and negligible for the Kuril group. TA had a highly negatively correlation with TSS:TA across all crops, across the foundation germplasm and for the Japanese and Russian groups and blueberry cultivars on their own, whereas the correlation was moderate for the Kuril group and strawberry cultivars and very high for the raspberry cultivars (**Figure 6.1**). Similarly, in Russian material, high and low TSS:TA were associated with low and high TA extremes, though intermediate TSS was observed in both cases (Petrushua 2009). Also, fruit pH had a moderate positive correlation with TSS:TA across crops and for the Japanese group on

216

Table 6.4. Foundation Germplasm: Pearson's correlations between biochemical determinations of fruit quality for blue honeysuckle and comparison crops in 2012/2013 in the Fraser Valley, BC, Canada (only statistically significant correlations [p < 0.05] are shown, DM – dry matter, TSS – total soluble solids, TA – titratable acidity, CAE – citric acid equivalents).

		Group	r			Group	r
DM (%)	TSS (%)	All Crops	0.840	TSS (%)	TSS:TA	All Foundation	0.596
		All Foundation	0.736			Japanese	0.703
		Japanese	0.723			Kuril	0.584
		Kuril	0.687			Russian	0.663
		Russian	0.589			Raspberry	0.672
		Blueberry	0.778			Strawberry	0.545
		Raspberry	0.654	TA (% CAE)	pH	All Foundation	*-0.542*
		Strawberry	0.777			Japanese	*-0.614*
	TA (% CAE)	Russian	*-0.362*			Russian	*-0.396*
		Raspberry	*-0.575*			Blueberry	*-0.795*
	pH	All Crops	*-0.455*			Raspberry	*-0.772*
		Kuril	*-0.509*			Strawberry	*-0.448*
		Raspberry	0.612		TSS:TA	All Crops	*-0.788*
	TSS:TA	All Foundation	0.485			All Foundation	*-0.820*
		Japanese	0.473			Japanese	*-0.862*
		Kuril	0.399			Kuril	*-0.686*
		Blueberry	0.538			Russian	*-0.871*
		Raspberry	0.641			Blueberry	*-0.855*
		Strawberry	0.604			Raspberry	*-0.927*
TSS (%)	TA (% CAE)	Japanese	*-0.389*			Strawberry	*-0.570*
		Raspberry	*-0.449*	pH	TSS:TA	All Crops	0.553
		Strawberry	0.364			All Foundation	0.437
	pH	All Crops	*-0.459*			Japanese	0.521
		Kuril	*-0.496*			Kuril	*-0.393*
						Russian	0.351
						Blueberry	0.753
						Raspberry	0.715
						Strawberry	0.477

its own. This correlation was low across the foundation germplasm and for the Russian group and strawberry cultivars but it was high for the blueberry and raspberry cultivars and, contrastingly, low and negative for the Kuril group.

The positive correlation between DM and TTS is based on the latter being a portion of the former. The positive relationship between DM and TSS:TA is due to TSS:TA being directly calculated from TSS. TA and, therefore, TSS:TA varies more independently of DM, which explains the lower correlation between TSS:TA and DM and higher correlation between TSS and DM. Within the Japanese group, genotypes with high TSS and low TA (J-21-78 and J-46-55) had high pH and TSS:TA as expected. The genotype with the highest TSS (J-66-53) had only moderate TA and pH, resulting in a moderate TSS:TA ratio. Low TSS was seen in association with high (J-444-39) or moderate TA (J-73-39), but moderate TSS was seen in association with high (J-22-14), moderate (J-41-83, J-42-45, J-43-87 and J-56-18) or low TA (J-45-14). Both pH and TSS:TA in the Japanese group corresponded with TA values: the former because of the direct biochemical connection between the two measures and the latter resulting from the greater importance of TA in determining TSS:TA across the foundation germplasm and for the Japanese group in particular.

Within the Kuril group, the genotype with the highest DM (K-97-12) also had the highest TSS and TA but the lowest TSS:TA. However, between the four late Kuril genotypes, there were no clear associations between DM, TSS, TA or TSS:TA as there was low variability for all of these FQ traits. Despite a greater degree of variation within the Russian group, there were no clear associations between DM, TSS, TA, pH or TSS:TA. Interestingly, the Japanese genotypes with the highest DM (J-21-78 and J-66-53) were also two of the highest for TSS, whereas one had low TA and the other moderate. Two genotypes (J-73-39 and J-444-39) with low DM also had low TSS, but another two (J-43-87 and J-22-14) had moderate TSS, while all four of these genotypes had moderate to high TA. Therefore, greater detail is obtained by comparing associations with the Japanese group, for which there was the strongest general association between high TSS and TA with low pH and TSS:TA. Specifically, TSS and TA had a loose negative association within the Japanese group, but these traits were positively correlated when compared across the foundation germplasm.

6.2.2 Potential Human Health Benefits of Foundation Germplasm

6.2.2.1 Description and Comparison of Foundation Germplasm Groups

The Russian group had the highest total phenolics (TP) on average, followed by the Kuril and then the Japanese group (643.6, 497.0 and 443.5 mg gallic acid equivalents [GAE]/100 g fresh weight (FW), respectively) (**Figure 6.2**; **Table 6.5**). In contrast to TP, Trolox Equivalence Antioxidant Capacity (TAC) assayed after 5 min of incubation was high for the Kuril and Russian groups and lower for the Japanese group (2.57, 2.58 and 1.92 mmol Trolox equivalents [TE/100 g FW, respectively). As for TP, FRAP assayed at 4 min of incubation was highest for the Russian group and lower for the Kuril group followed by the Japanese group (7.19, 6.41 and 5.12 mmol AAE/100 g FW, respectively).

The absolute range in TP was greatest for the Russian group, about half as broad for the Japanese group and half again for the Kuril group (314.2, 204.2 and 101.5 mg GAE/100 g FW, respectively). For TAC, the absolute ranges were similar for the Japanese and Russian groups and lower for the Kuril group (1.34, 1.31 and 0.57 mmol TE/100 g FW, respectively). For FRAP, the range was greatest for the Russian group, followed by the Kuril and Japanese groups (3.36, 2.04 and 1.71 mmol AAE/100 g FW, respectively).

Within the Japanese group, J-22-14 had the lowest TP (364.8 mg GAE/100 g FW), followed by J-41-83, J-73-39 and J-46-55, while J-43-87 (568.9 mg GAE/100 g FW) had the highest, followed by J-56-18 (**Appendix D.4**; **Appendix D.5**). For TAC, J-66-53 was the lowest (1.28 mmol TE/100 g FW), followed by J-45-14, whereas J-56-18 (2.63 mmol TE/100 g FW) was significantly higher than the remaining intermediate genotypes. Only the top few Japanese genotypes were equivalent to the lowest Kuril and Russian genotypes, but J-56-18 was not significantly higher than any genotype in these other groups. For FRAP, J-21-78, J-41-83, J-45-14, J-46-55, J-66-53 and J-73-39 (4.54-4.82 mmol AAE/100 g FW) were the lowest across the foundation germplasm, were statistically equivalent to one another and significantly lower than any of the Kuril and Russian genotypes. The more intermediate genotypes, J-22-14, J-42-45, J-43-87 and J-444-39, were equivalent to some of the lowest Kuril and Russian genotypes. J-56-18 (6.25 mmol AAE/100 g FW) was the highest in the Japanese group and was statistically higher than K-3-03 and equivalent to several other Kuril and Russian genotypes. For TAC and FRAP, similar observations were made when assays were conducted at 15 and 14 min, respectively (**Appendix D.3**; **Appendix D.6; Appendix D.7**).
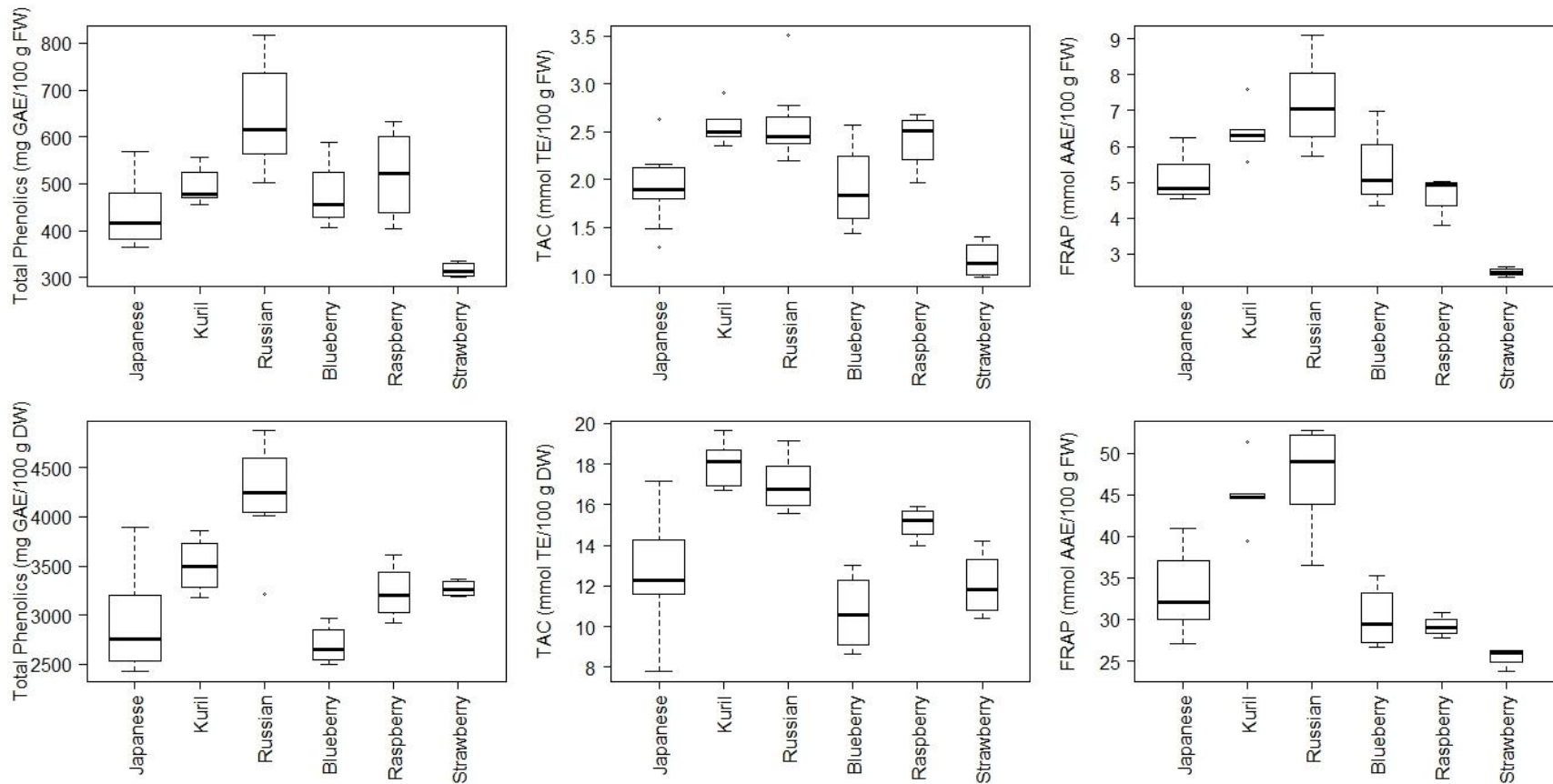
Figure 6.2. Foundation Germplasm: Nutritional content in blue honeysuckle and comparison crops in 2012/2013 in the Fraser Valley, BC, Canada (FW – fresh weight, DW – dry weight, GAE – gallic acid equivalents, TAC – Trolox antioxidant capacity, TE – Trolox equivalents, FRAP – ferric reducing antioxidant potential, AAE – ascorbic acid equivalents, boxplot widths are proportional to the square root of the sample size for each group).

Table 6.5. Foundation Germplasm: Nutritional content in blue honeysuckle and comparison crops in 2012/2013 in the Fraser Valley, BC, Canada (FW – fresh weight, DW – dry weight, GAE – gallic acid equivalents, TE – Trolox equivalents, AAE – ascorbic acid equivalents).

	Group	Japanese	Kuril	Russian	Blueberry	Raspberry	Strawberry	Japanese	Kuril	Russian	Blueberry	Raspberry	Strawberry
		mg GAE/100 g FW						mg GAE/100 g DW					
Total Phenolics	Average	443.5	497.0	643.6	477.0	519.7	316.3	2899.3	3510.4	4231.2	2694.4	3231.2	3273.0
	Median	416.2	478.3	615.4	456.5	520.9	314.3	2750.2	3496.6	4247.8	2651.8	3199.6	3265.8
	Minimum	364.8	455.8	501.8	406.7	405.1	301.6	2425.2	3178.2	3207.3	2503.1	2919.1	3189.0
	Maximum	568.9	557.3	816.0	588.2	632.0	335.0	3888.3	3859.4	4879.3	2970.7	3606.7	3371.3
	Range	204.2	101.5	314.2	181.6	226.8	33.4	1463.1	681.2	1672.0	467.6	687.6	182.2
		mmol TE/100 g FW at 5 min						mmol TE/100 g DW at 5 min					
Total Antioxidant Capacity	Average	1.9	2.6	2.6	1.9	2.4	1.2	12.6	18.0	17.0	10.7	15.1	12.1
	Median	1.9	2.5	2.5	1.8	2.5	1.1	12.3	18.1	16.8	10.6	15.2	11.8
	Minimum	1.3	2.3	2.2	1.4	2.0	1.0	7.8	16.7	15.5	8.6	14.0	10.4
	Maximum	2.6	2.9	3.5	2.6	2.7	1.4	17.2	19.7	19.1	13.0	15.9	14.2
	Range	1.3	0.6	1.3	1.1	0.7	0.4	9.4	3.0	3.6	4.4	1.9	3.8
		mmol AAE/100 g FW at 4 min						mmol AAE/100 g DW at 4 min					
Ferric Reducing Antioxidant Potential	Average	5.1	6.4	7.2	5.4	4.7	2.5	33.6	45.0	47.4	30.2	29.2	25.5
	Median	4.8	6.3	7.0	5.1	4.9	2.5	32.1	44.7	48.9	29.4	29.1	26.0
	Minimum	4.5	5.6	5.7	4.3	3.8	2.4	27.0	39.5	36.5	26.6	27.7	23.7
	Maximum	6.3	7.6	9.1	7.0	5.0	2.6	40.9	51.4	52.7	35.3	30.9	26.3
	Range	1.7	2.0	3.4	2.7	1.2	0.3	13.9	11.9	16.2	8.6	3.1	2.5

Within the Kuril group, K-3-07 had significantly higher TP (557.3 mg GAE/100 g FW) than K-3-05, K-3-06 and K-97-12, whereas K-3-03 was intermediate. The lowest Kuril genotypes were significantly higher than the three lowest Japanese genotypes, while the highest Kuril genotypes were statistically equivalent to all but the two highest Russian genotypes. For TAC, K-97-12 (2.91 mmol TE/100 g FW) was significantly higher than all except K-3-06. The four late genotypes were not significantly different from one another and were equivalent to all the Russian genotypes except for R-2-16 (3.51 mmol TE/100 g FW). K-97-12 had significantly higher TAC than R-2-07, R-2-11, R-2-14, R-27-35 and all but the highest Japanese genotype, but it still had significantly lower TAC than R-2-16. For FRAP, K-3-03 (5.55 mmol AAE/100 g FW) was lower than K-3-06, K-3-07 and K-97-12, but was equivalent to R-2-11 and R-27-35. K-3-05, K-3-06 and K-3-07 were statistically equivalent to one another and several of the low and intermediate Russian genotypes but were lower than K-97-12. Of note, K-3-07 was higher than R-27-35, the lowest in the Russian group. Further, K-97-12 (7.59 mmol AAE/100 g FW) was statistically higher than the rest of the Kuril group, all Japanese genotypes as well as R-2-07, R-2-11 and R-27-35, but it was equivalent to all other Russian genotypes except R-2-16.

Within the Russian group, R-27-35 had the lowest TP (501.8 mg GAE/100 g FW), followed by R-2-11 and R-2-14. R-2-06, R-2-07 and R-2-10 were intermediate but only significantly greater than R-27-35. R-2-13 was significantly greater than all but R-2-06. R-2-16 (815.2 mg GAE/100 g FW) was significantly greater than all but R-2-13. Only R-2-13 and R-2-16 were significantly greater than all Japanese and Kuril genotypes. The lowest Russian genotype (R-27-35) was equivalent to the highest Japanese genotypes and all the Kuril genotypes though greater than several of the lowest Japanese genotypes. For TAC, all were statistically equivalent except for R-2-16, which was statistically higher than any other genotype across crops (**Section 6.2.2.2**). For FRAP, R-27-35 was the lowest (5.73 mmol AAE/100 g FW), but R-2-07, R-2-11 and R-2-14 were also quite low. R-2-06 and R-2-11 were relative intermediates that were lower than R-2-13 and R-2-16, which were the highest blue honeysuckle genotypes.

Overall, the genotypes with the lowest TP, TAC and FRAP were Japanese, and the highest were Russian. For TP, there was considerable overlap between the lower Japanese and intermediate Kuril genotypes, but the overlap between the Russian group and the other two foundation groups was less substantial. For TAC, there was not much overlap between the Japanese group and the other foundation groups, but there was substantial overlap between the

Kuril and Russian groups. In contrast, for FRAP, there was extensive overlap between the Japanese and Kuril groups and between the Kuril and Russian groups, but only slight overlap between the low Japanese and high Russian group.

Across the foundation germplasm, the Japanese and Russian groups had the lowest and highest average TP, TAC and FRAP, respectively, while the Kuril group was intermediate. Within each group, relative comparisons between genotypes varied for TP, TAC and FRAP. For TP, the absolute range was 50% greater for the Russian than the Japanese group, which was still two times that seen for the Kuril group. The broader range in TP for the Russian group is understandable since several ssp. are included in this foundation group and flavonoid content is known to vary considerably across species and cultivars. Whereas the highest and lowest values were in the Russian and Japanese groups, respectively, only the Japanese group overlapped completely with the intermediate Kuril group, the Russian group not having as low an extreme.

For TAC, the Japanese and Russian groups had similar absolute ranges, which were more than two times that seen for the Kuril group. In contrast, for FRAP, the Russian group's range was twice as great as for the Japanese group, and the Kuril group's range was intermediate. As for TP, the genotypes with the highest and lowest TAC were Russian and Japanese, respectively. In contrast to TP, the Russian group completely overlapped the extremes of the intermediate Kuril group, whereas the Japanese group did not have as high an extreme as the Kuril group. When compared on a DW basis, TAC was slightly higher for the Kuril group than for the Russian group though their absolute ranges were narrow compared to the Japanese group with its much lower average. The highest FRAP was found in the Russian group and the lowest in the Japanese group, as expected, but neither group's range overlapped fully with the intermediate Kuril group. The high degree of variability within the Kuril group resulted in a higher extreme than in the Japanese group and a lower extreme than in the Russian group. When calculated on a DW basis (**Figure 6.2**; **Table 6.5**), these relative comparison and absolute group ranges were the same as for FW calculations.

6.2.2.2 Blueberry, Raspberry and Strawberry Compared to Foundation Germplasm

Average blueberry TP (477.0 mg GAE/100 g FW) was intermediate to the averages for the Kuril and Japanese groups, whereas the absolute range was as broad as seen for the Japanese group (**Figure 6.2**; **Table 6.5**). In contrast, average TP (519.7 mg GAE/100 g FW) for raspberry was

higher than the average for the Japanese or Kuril groups but not higher than for the Russian group, and the range was slightly broader and narrower than for the Japanese and Russian groups, respectively (**Appendix D.4**; **Appendix D.5**). With a very narrow absolute range, the average strawberry TP (316.3 mg GAE/100 g FW) was lower than the average for any foundation group or any blue honeysuckle, blueberry or raspberry genotype for that matter.

For blueberry, 'Reka' had the lowest TP (406.7 mg GAE/100 g FW), which was equivalent to the low and intermediate Japanese and Kuril genotypes. 'Bluecrop' and 'Duke' had higher TP than the lowest Japanese genotype but were equivalent to all but the highest Kuril genotype (K-3-07) and lower than all Russian genotypes except for R-27-35. 'Elliott' (588.2 mg GAE/100 g FW) had significantly higher TP than any other blueberry cultivar, most of the Japanese genotypes, all but K-3-03 and K-3-07 in the Kuril group and even R-27-25 in the Russian group. R-2-06, R-2-07, R-2-10, R-2-11 and R-2-14 were all equivalent to 'Elliott', while only R-2-13 and R-2-16 were significantly higher. In comparison to raspberry, 'Reka', 'Duke' and 'Bluecrop' were the same as 'Cascade Bounty' and 'Chemainus' but lower than 'Meeker' and 'Saanich', whereas 'Elliott' was equivalent to 'Meeker' and 'Saanich'. In comparison to strawberry, 'Bluecrop', 'Duke' and 'Elliott' were higher than all four strawberry cultivars, but 'Reka' was not significantly different from 'Totem' though higher than 'Puget Reliance', 'Rainier' and 'Stolo'.

For raspberry, 'Cascade Bounty' (405.1 2 mg GAE/100 g FW) was equivalent to the lowest Japanese genotype and significantly lower than the highest genotypes in each foundation group. 'Chemainus' (470.3 mg GAE/100 g FW) had higher TP than some of the lower Japanese genotypes, but was not significantly different from the intermediate Japanese and Kuril genotypes or the two lowest Russian genotypes. Of note, there were blue honeysuckle genotypes in each foundation group with significantly higher TP than 'Chemainus'. 'Meeker' (571.6 mg GAE/100 g FW) was equivalent to the highest Japanese and Kuril genotypes as well as most of the Russian group, but it was significantly lower than only R-2-13 and R-2-16 and higher than R-27-35. 'Saanich' (632.0 mg GAE/100 g FW) was higher than all the Kuril genotypes and all but J-43-87 in the Japanese group, comparing to the Russian group as 'Meeker' did. All four raspberry cultivars had significantly higher TP than all four strawberry cultivars, and there were no significant differences between strawberry cultivars, which were equivalent to the lowest Japanese genotypes but lower than all Kuril and Russian genotypes.

With nearly as broad a range as the Japanese and Russian groups, the average blueberry TAC (1.92 mmol TE/100 g FW) was equal to the Japanese average but lower than the Kuril and Russian averages. The raspberry average (2.41 mmol TE/100 g FW) was higher than the Japanese group average but slightly below the Kuril and Russian averages, while the range was modest compared to blueberry. As for TP, the average strawberry TAC (1.16 mmol TE/100 g FW) was far lower than for any blue honeysuckle foundation group or any other crop genotype, and the range was even more modest than that of raspberry.

As for TP, the lowest blueberry TAC was seen for 'Reka' (1.43 mmol TE/100 g FW), which was equivalent to the lowest blue honeysuckle (J-66-53) but significantly lower than most of the Japanese genotypes and all the Kuril and Russian genotypes. 'Bluecrop' (1.75 mmol TE/100 g FW) had significantly higher TAC than the lowest Japanese genotype but was still significantly lower than all Kuril and Russian genotypes, and 'Duke' (1.92 mmol TE/100 g FW) compared similarly. 'Elliott' (2.57 mmol TE/100 g FW) was significantly higher than all the Japanese genotypes, except J-56-18, but was the same as all Kuril and Russian genotypes except for the highest extreme, R-2-16. 'Reka' had lower TAC than all raspberry cultivars, 'Bluecrop' and 'Duke' were equivalent to 'Cascade Bounty' but significantly lower than the rest and 'Elliott' was equivalent to 'Chemainus', 'Meeker' and 'Saanich'. Similarly, 'Reka' was as low as 'Stolo' and 'Totem' but significantly higher than 'Puget Reliance' and 'Rainier', and the other three blueberry cultivars were higher than all strawberry cultivars.

For raspberry, 'Cascade Bounty' (1.97 mmol TE/100 g FW) had significantly higher TAC than the lowest two Japanese genotypes but was equivalent to most Japanese genotypes, falling just short of the Kuril group and equalling the two lowest Russian genotypes (R-2-11 and R-2-14). 'Chemainus', 'Meeker' and 'Saanich' (2.56, 2.67 and 2.45 mmol TE/100 g FW, respectively) had significantly higher TAC than all Japanese genotypes, except J-56-18, while being equivalent to the four late Kuril genotypes and all but R-2-16 in the Russian group. Only 'Meeker' was equal to K-97-12. All raspberry cultivars had significantly greater TAC than the strawberry cultivars, which had a narrow absolute range. 'Rainier' (0.98 mmol TE/100 g FW) was lower than all blue honeysuckle genotypes. 'Puget Reliance' (1.03 mmol TE/100 g FW) was equivalent to only J-66-53, while 'Stolo' and 'Totem' (1.22 and 1.40 mmol TE/100 g FW, respectively) were equivalent to only J-66-53 and J-45-14. No strawberry cultivar had equivalent TAC to any Kuril or Russian genotype.

Average blueberry FRAP (5.36 mmol AAE/100 g FW) was closest to the lower Japanese average, but the absolute range was intermediate to the Kuril and Russian groups in breadth. Average raspberry FRAP (4.66 mmol AAE/100 g FW) was lower than for all three foundation groups, and the range was more modest. For strawberry, the average (2.48 mmol AAE/100 g FW) was lower and the range was narrower than observed for blueberry and raspberry or for any blue honeysuckle group.

As for TP and TAC, 'Reka' had the lowest FRAP (4.32 mmol AAE/100 g FW), equalling the lowest Japanese genotype and being statistically lower than any Kuril or Russian genotype. 'Bluecrop' (4.98) and 'Duke' (5.12 mmol AAE/100 g FW) had statistically higher FRAP than 'Reka', while they were still not different from the lowest Japanese genotypes but lower than all but the very lowest Kuril and Russian genotypes. 'Elliott' had significantly higher FRAP than any of the Japanese genotypes, all but K-3-07 and K-97-12 in the Kuril group and even the lowest two Russian genotypes (R-27-35 and R-2-11). Therefore, statistical equivalence with K-97-12, R-2-06, R-2-07, R-2-10 and R-2-14 makes 'Elliott' comparable with the upper end of the blue honeysuckle germplasm as only R-2-13 and R-2-16 were still statistically higher. For context, 'Reka' was equivalent to 'Cascade Bounty' but was lower than the other three raspberry cultivars. 'Bluecrop' and 'Duke' were equivalent to 'Chemainus', 'Meeker' and 'Saanich' but greater than 'Cascade Bounty'. 'Elliott' was higher than any of the raspberry cultivars, and all blueberry cultivars were significantly higher than all strawberry cultivars.

For raspberry, 'Cascade Bounty' (3.81 mmol AAE/100 g FW) had lower FRAP than any blue honeysuckle genotype, whereas 'Chemainus' (4.96 mmol AAE/100 g FW), 'Meeker' (5.03 mmol AAE/100 g FW) and 'Saanich' (4.86 mmol AAE/100 g FW) were equivalent to the low and intermediate Japanese genotypes, but only 'Meeker' was equivalent to the lowest Kuril genotype (K-3-03) and none were equal to any of the Russian genotypes. All raspberry cultivars and blue honeysuckle genotypes had significantly higher FRAP than the strawberry cultivars, between which there were no statistical differences.

The range of inference for literature reports comparing TP and AOA between blue honeysuckle genotypes as well as against other niche crops is limited due to lack of biological replication and use of narrow subsets of foundation groups. Further, comparison across regions is problematic because of differences between studies in environments (e.g., climate, soil) and methods (e.g., sample collection, extraction and assay procedure). The current study is the first

comparison of a broad range of blue honeysuckle germplasm against large-scale commercial crops using biological replication (i.e., side-by-side field plantings). Additionally, it was conducted in a temperate climate suited to large-scale fruit production.

Evaluation in the Fraser Valley builds on a preliminary analysis in a similar region (Corvallis, Oregon) that compared blue honeysuckle genotypes across five ssp. with representatives from all three foundation groups (Thompson and Chaovanalikit 2003). Without biological replication and only 11 genotypes, differences within and between genetic groups were not interpreted, but the range in TP (440-1,142 mg GAE/100 g FW) was close to that of the current study. A higher extreme in TP was due to inclusion of a wild diploid relative, *L. boczkarnivokae*, which has small, unpalatable fruit and is not representative of current blue honeysuckle germplasm resources. Direct comparison with FRAP measured in this study is not possible due to the use of a different standard. In another unreplicated comparison, blue honeysuckle had the highest TP (1,111.17 mg GAE/100 g FW) and TAC (9.55 mmol TE/100 g FW) of 14 non-commercial fruit species in Western Canada (Bakowska-Barczak et al 2007). This study's measure of TP was near the upper extreme observed in Corvallis, but its measure of TAC was more than three times higher than in the current study. In contrast, wild raspberry and strawberry were only slightly higher than their domesticated counterparts presented here. This discrepancy is due to the use of a minor Russian taxon (ssp. *pallasii*), with small, unpalatable fruit, which is also non-representative of primary blue honeysuckle germplasm.

In the Czech Republic, a Russian accession had considerably lower TP (140.5 mg GAE/100 g FW) than in the current study (Palíková et al 2008). In contrast, another Czech study of Russian material concurred with the current study, TP ranging from 575-903 mg GAE/100 g FW (Rop et al 2011). Equally, unreplicated measures of 19 Russian cultivars in Poland showed a nearly identical range in TP (554.2-865.9 mg GAE/100 g FW) (Sochor et al 2014). These latter two studies included 'Morena' (R-2-06) and 'Nimfa' (R-2-07), measuring only 15 and 4% lower, respectively (Rop et al 2011), and 5% lower and 4% higher, respectively (Sochor et al 2014), than in the current study. In central Poland, eight Russian accessions had TAC ranging from slightly lower to more than twice as high (12.65-49.73 mmol TE/100 g DW) as the Russian group in the current study (Wojdyło et al 2013). Similarly, in northern Poland, the range in TP (2,270-5,290 mg GAE/100 g DW) for five Russian genotypes overlapped the range for the Russian group in the current study but had a lower average, whereas only the lower extreme in TAC (16.9-41.7 mmol

TE/100 g DW) overlapped with that of the current study (Kusznierewicz et al 2012). This range in TP was slightly higher and lower than wild bilberries (*Vaccinium myrtillus* L.) and bog bilberries (*Vaccinium uliginosum* L.), respectively, these comparison crops having intermediate TAC to blue honeysuckle. Another comparison of Russian germplasm to niche crops in Poland found two times higher TP than black currant (*Ribes nigrum* L.) and black mulberry (Morus nigra L.), which was lower than for bilberry (*Vaccinium myrtillus* L.), European juneberry (*Amelanchier ovalis* Medik.) and blackberry (*Rubus plicatus* Weihe & Nees) (Zadernowski et al 2005). These findings were lower than for any blue honeysuckle or comparison crop in the current study.

A Polish cultivar of Russian descent had intermediate TP (540.0 mg GAE/100 g FW), TAC (5.15 mmol TE/100 g FW) and FRAP (4.92 mmol TE/100 g FW) compared to 30 fruit species (Podsędek et al 2014). Specifically, though lacking biological replication, this is the first comparison to blueberry (lowbush (*Vaccinium angustifolium* Ait.) as opposed to highbush blueberry (*Vaccinium corymbosum* L.)), raspberry and strawberry in the literature. TP, TAC and FRAP measured 1.6, 1.9 and 2.9 times greater than blueberry, 2.8. 2.5 and 2.9 greater than raspberry and 2.8, 3.1 and 5.0 times greater than strawberry, respectively. Compared to the current findings, TP was near the lower extreme of the Russian group. Blue honeysuckle TAC was about 50% higher than the highest Russian extreme, while blueberry, raspberry and strawberry TAC were almost identical, 25% lower and 18% higher, respectively, than the upper extremes of their counterparts in the current study. FRAP was not directly comparable due to use of different standards. Therefore, a minority of studies show wider, lower or higher ranges, but the current biologically replicated data provide statistical validation for similar ranges in TP and AOA observed in several regions. Further, the current study provides replicated data for all three foundation groups in a temperate climate, and it is directly comparable to three large-scale commercial crops.

Relative comparisons to other commercial crops varied between TP and measures of AOA as well as whether they were calculated on a FW or DW basis. For TP on a FW basis, the lowest blue honeysuckle was 8.9% higher than the highest strawberry. The highest Kuril genotype was 11.8% lower than the highest raspberry and the highest Russian was 38.7% higher than the highest blueberry. On a DW basis, the lowest blue honeysuckle was 3.1% lower than the highest blueberry, the highest Kuril genotype was only 7.0% higher than the highest raspberry and the highest Russian was 44.7% higher than the highest strawberry. For TAC, the lowest Japanese

genotype was 8.6% lower than the highest strawberry on a FW basis but was 10.0% lower than even the lowest blueberry on a DW basis. The highest Kuril genotype was 1.8% lower than the highest raspberry and the highest Russian genotype was 36.4% higher than the highest blueberry on a FW basis. However, the highest Japanese genotype was only 7.9% higher than the highest raspberry and the highest Russian genotype was 38.3% higher than the highest strawberry. For FRAP, the lowest Japanese genotype was 72.9 and 2.9% higher than the highest strawberry on a FW and DW basis, respectively. The highest Japanese genotype was 10.6% lower and 16.1% higher than the highest blueberry on a FW and DW basis, respectively, whereas the highest Kuril was 81.0 and 70.8% higher than the highest raspberry on a FW and DW basis, respectively.

Therefore, while relative differences between blue honeysuckle groups were similar on a FW and DW basis, blueberry TP was relatively high on a FW basis and low on a DW basis, the opposite being true of strawberry (**Section 6.2.1.2**). Blueberry had relatively higher values for FRAP than TAC compared to raspberry and strawberry, and FW and DW calculations of TAC and FRAP compared similarly across blue honeysuckle foundation groups.

6.2.2.3 Out-group Comparisons to Foundation Germplasm

J-PP had equivalent TP (521.2 mg GAE/100 g FW) to the highest Japanese genotype but had equivalent TAC (1.86 mmol TE/100 g FW) and FRAP (4.94 mmol AAE/100 g FW) to more intermediate Japanese germplasm (**Appendix D.4**; **Appendix D.5**).

'Borealis', 'Tundra' and 'Indigo Gem' were equivalent for TP (477.9, 477.2 and 502.2 mg GAE/100 g FW, respectively) and TAC (2.35, 2.52 and 2.48 mmol TE/100 g FW, respectively). These TP values were close to the intermediate and higher Japanese and Kuril genotypes, including K-97-12, as well as the lowest Russian genotypes (R-2-11, R-2-14 and R-27-35). Their TAC values were the same as all Russian genotypes, except R-2-16, the highest Japanese genotypes and the four late Kuril genotypes, while only 'Tundra' and 'Indigo Gem' were as high as K-97-12. For FRAP, 'Borealis' (6.89 mmol AAE/100 g FW) was statistically equivalent to the highest Japanese and Kuril genotypes as well as most Russian genotypes, except the very lowest (R-27-35) and two highest (R-2-13 and R-2-16). 'Indigo Gem' (6.96 mmol AAE/100 g FW) was equivalent to 'Borealis' and similar to the Russian and Kuril groups but was higher than the highest Japanese genotype. 'Tundra' had significantly greater FRAP than either 'Borealis' or 'Indigo Gem' and all other genotypes except R-2-13 and R-2-16 to which it was equivalent.

229

In Eastern Canada, comparison with partridge berry, lowbush blueberry, grape, strawberry, raspberry and blackberry showed 'Borealis' to have significantly greater TP than 'Tundra' or 'Indigo Gem' (622.52, 500.78 and 428.14 mg GAE/100 g, respectively) (Rupasinghe et al 2012). These results were in the same range as the current study, which showed no statistical differences between cultivars. The University of Saskatchewan (U of S) cultivars had two to four times higher TP than the lowbush blueberry and raspberry and two to three times higher TP than strawberry, which were much greater differences than seen in the current study. 'Tundra' had lower FRAP than 'Borealis' or 'Indigo Gem' (27.96, 46.38 and 46.90 mmol TE/100 g FW, respectively), which also contrasted with the current findings. Direct numerical comparisons are not possible due to use of different standards, but this report shows that 'Borealis' and 'Indigo Gem' have up to six times higher FRAP than raspberry and strawberry and three times higher FRAP than lowbush blueberry, which are also much greater differences than in the current study. While genotype by environment interactions likely affect the relative TP and AOA between crops, the current study, using direct comparison in the field with biological replication, contradicts much higher values produced in unreplicated comparisons of fruit obtained from disparate sources.

6.2.2.4 Correlations between Potential Human Health Benefits Traits

For all three assays, FW and DW calculations of each assay had high to very high positive correlations across all crops and across the blue honeysuckle foundation groups combined and separate (**Table 6.6**). For the comparison crops, these correlations were also high to very high, except for TP in strawberry and FRAP in raspberry and strawberry for which the correlations were moderate. Across all four crops, positive correlations between assays were moderate to high. Across the foundation germplasm, the correlation was low between TP and TAC, moderate between TP and FRAP and high between TAC and FRAP. These correlations ranged from low to moderate for the Japanese group, negligible to moderate for the Kuril group, moderate to high for the Russian group, high to very high for blueberry and moderate to high for raspberry and strawberry. In general, these strong correlations confirm findings for other species (Chen et al 2014) and for blue honeysuckle (Kusznierewicz et al 2012; Sochor et al 2014; Rupasinghe et al 2012), confirming the important role of phenolics in the *in vitro* reducing capacity of blue honeysuckle fruit.

Table 6.6. Foundation Germplasm: Pearson's correlations between nutritional content traits for blue honeysuckle and comparison crops in 2012/2013 in the Fraser Valley, BC, Canada (only statistically significant correlations [$p < 0.05$] are shown, FW – fresh weight, DW – dry weight, TP – total phenolics, GAE – gallic acid equivalents, TAC – Trolox antioxidant capacity, TE – Trolox equivalents, FRAP – ferric reducing antioxidant potential, AAE – ascorbic acid equivalents).

		Group	r			Group	r
TP (mg GAE/100 g FW)	TP (mg GAE/100 g DW)	All Crops	0.763	TP (mg GAE/100 g FW)	FRAP (mmol AAE/100 g FW) at 4 min	All Crops	0.634
		All Foundation	0.920			All Foundation	0.526
		Japanese	0.939			Japanese	0.584
		Kuril	0.920			Kuril	0.343
		Russian	0.824			Russian	0.837
		Blueberry	0.773			Blueberry	0.928
		Raspberry	0.824			Raspberry	0.622
		Strawberry	0.680			Strawberry	0.618
	TAC (mmol TE/100 g FW) at 5 min	All Crops	0.628		FRAP (mmol AAE/100 g DW) at 4 min	All Crops	0.421
		All Foundation	0.475			All Foundation	0.371
		Japanese	0.427			Japanese	0.468
		Russian	0.614			Russian	0.599
		Blueberry	0.741			Blueberry	0.679
		Raspberry	0.612			Strawberry	0.485
		Strawberry	0.774		TAC (mmol TE/100 g DW) at 5 min	All Crops	0.839
	TAC (mmol TE/100 g DW) at 5 min	All Crops	0.382			All Foundation	0.920
		All Foundation	0.345			Japanese	0.954
		Japanese	0.335			Kuril	0.942
		Russian	0.476			Russian	0.811
		Blueberry	0.498			Blueberry	0.923
		Strawberry	0.601			Raspberry	0.749
						Strawberry	0.910

Table 6.6. Continued. Foundation Germplasm: Pearson's correlations between nutritional content traits for blue honeysuckle and comparison crops in 2012/2013 in the Fraser Valley, BC, Canada (p < 0.05, FW – fresh weight, DW – dry weight, TP – total phenolics, GAE – gallic acid equivalents, TAC – Trolox antioxidant capacity, TE – Trolox equivalents, FRAP – ferric reducing antioxidant potential, AAE – ascorbic acid equivalents).

		Group	r
TAC (mmol TE/100 g FW) at 5 min	FRAP (mmol AAE/100 g FW) at 4 min	All Crops	0.759
		All Foundation	0.703
		Japanese	0.591
		Kuril	0.618
		Russian	0.768
		Blueberry	0.862
		Raspberry	0.896
		Strawberry	0.434
	FRAP (mmol AAE/100 g DW) at 4 min	All Crops	0.593
		All Foundation	0.579
		Japanese	0.544
		Kuril	0.419
		Russian	0.319
		Blueberry	0.754
		Raspberry	0.576
		Strawberry	0.545
FRAP (mmol AAE/100 g FW) at 4 min	FRAP (mmol AAE/100 g DW) at 4 min	All Crops	0.870
		All Foundation	0.897
		Japanese	0.906
		Kuril	0.914
		Russian	0.765
		Blueberry	0.831
		Raspberry	0.693
		Strawberry	0.530

The correlations between assays within foundation groups could not be interpreted for the Russian or Kuril groups due to complex interactions with fruit shapes and sizes in the former group and to lack of variability in the latter. In contrast, correlations within the Japanese group were interpretable. The genotype with the highest TP (J-56-18) also had the highest TAC and FRAP though another two (J-43-87 and J-444-39) had moderate TAC and FRAP. Therefore, Japanese genotypes with low or moderate TP had low or moderate TAC and FRAP and, when compared on a DW basis, these tendencies were slightly more consistent. The Japanese genotypes with higher DM tended to have the lower TAC and FRAP on a DW basis, but there was no consistent trend between DM and TP calculated on a DW basis. While the Japanese group had low TP, TAC and FRAP compared to the other foundation groups, the relative association between TP and TAC or FRAP was not obvious within the Japanese group.

6.2.3 Fruit Quality Traits in Improved Germplasm
6.2.3.1 Parent Genotype Contrasts for Improved Germplasm Families

For DM and TSS in eight Japanese/Kuril families, the Japanese parent was significantly higher than the Kuril parent for six and two, respectively (**Appendix D.8**). For TA and pH, the Japanese parent was higher for two and five families, respectively, whereas the Kuril parent was higher for one family for TA and two families for pH. For TSS:TA, the Japanese and Kuril parents were higher for two and five families, respectively. For DM and TSS in the 16 Japanese/Russian families, the Russian parent was only higher for one family each, and the Japanese parent was higher for six and five families, respectively. For TA and pH, the Japanese parent was higher for twelve and one family, respectively, compared to three and seven for the Russian parent. For TSS:TA, the Russian parent was higher for thirteen families. For DM and TSS in the 16 Kuril/Russian families, the Russian parent was higher for eleven and three families, respectively. For TA and pH, the Kuril parent was higher for six and seven families, respectively, and the Russian parent was higher for four and five families, respectively. For TSS:TA, the Kuril and Russian parents were higher for two and eight families, respectively. Therefore, the Russian parent more often had higher DM and TSS than either the Japanese or Kuril parent when statistical differences could be determined, whereas the Japanese parent more often had higher DM and TSS than the Kuril parent. In contrast, the Japanese parent more often had higher TA than the Kuril or Russian parent, but the Russian and Kuril parents were not a strong contrast. Correspondingly,

233

there was no consistent contrast between the Kuril and Russian parents for pH, but they more often had higher pH than the Japanese parent. For TSS:TA, the Russian parents' high ratios contrasted more distinctly with the Japanese parents' lower ratios than with the Kuril parents' relatively intermediate ratios, whereas the Kuril parent more often had a higher ratio than the Japanese parent.

6.2.3.2 Absolute Range, Group Extremes and Heritability

The lowest DM (12.4%), TA (1.53%) and pH (2.65) were in the Kuril/Russian group, but the lowest TSS (8.5%) and TSS:TA (2.73) were in the Japanese/Russian and Japanese/Kuril groups, respectively (**Figure 6.3**; **Table 6.7**). Compared to the Kuril/Russian group, the Japanese/Kuril and Japanese/Russian groups had nearly as low extremes in DM (13.0% each), TA (1.61 and 1.60%) and pH (2.71 and 2.79). The Japanese/Kuril and Kuril/Russian groups had nearly as low extremes in TSS (8.9 and 8.7%) as Japanese/Russian group. The Japanese/Russian group had a similar TSS:TA extreme (2.91) to the Japanese/Kuril group, but the Kuril/Russian group's extreme was much less pronounced (3.48).

The highest DM (17.5%) and TA (3.54%) were in the Japanese/Russian group, TSS (12.9%) in the Japanese/Kuril and Japanese/Russian groups, pH (3.45) in the Kuril/Russian group and TSS:TA (7.09) in the Japanese/Kuril group. Both the Japanese/Kuril and Kuril/Russian extremes were nearly as high for DM (16.9 and 16.2%), but only the former was close for TA (3.36%), the latter being substantially lower (2.89%). The Kuril/Russian group's highest TSS extreme was not far behind the other foundation groups (12.1%). In contrast, the Japanese/Kuril and Japanese/Russian groups had considerably lower extremes in pH (3.16 and 3.18). The Japanese/Russian and Kuril/Russian groups had nearly as high extremes in TSS:TA (7.04 and 6.87).

For DM, the absolute range in the Japanese/Kuril (3.9%) and Kuril/Russian groups (3.8%) were similar to one another and somewhat narrower than for the Japanese/Russian group (4.4%). For TSS and TA, the Kuril/Russian group had the narrowest (3.36 and 1.36%) and the Japanese/Russian group the broadest (4.38 and 1.94%) ranges, the Japanese/Kuril varying more moderately (3.98 and 1.75%). For pH, the Japanese/Russian group had the most restricted range (0.39), followed closely by the Japanese/Kuril group (0.45) and dwarfed by the broad Kuril/Russian range (0.80). For TSS:TA, the Kuril/Russian group had the most restricted range
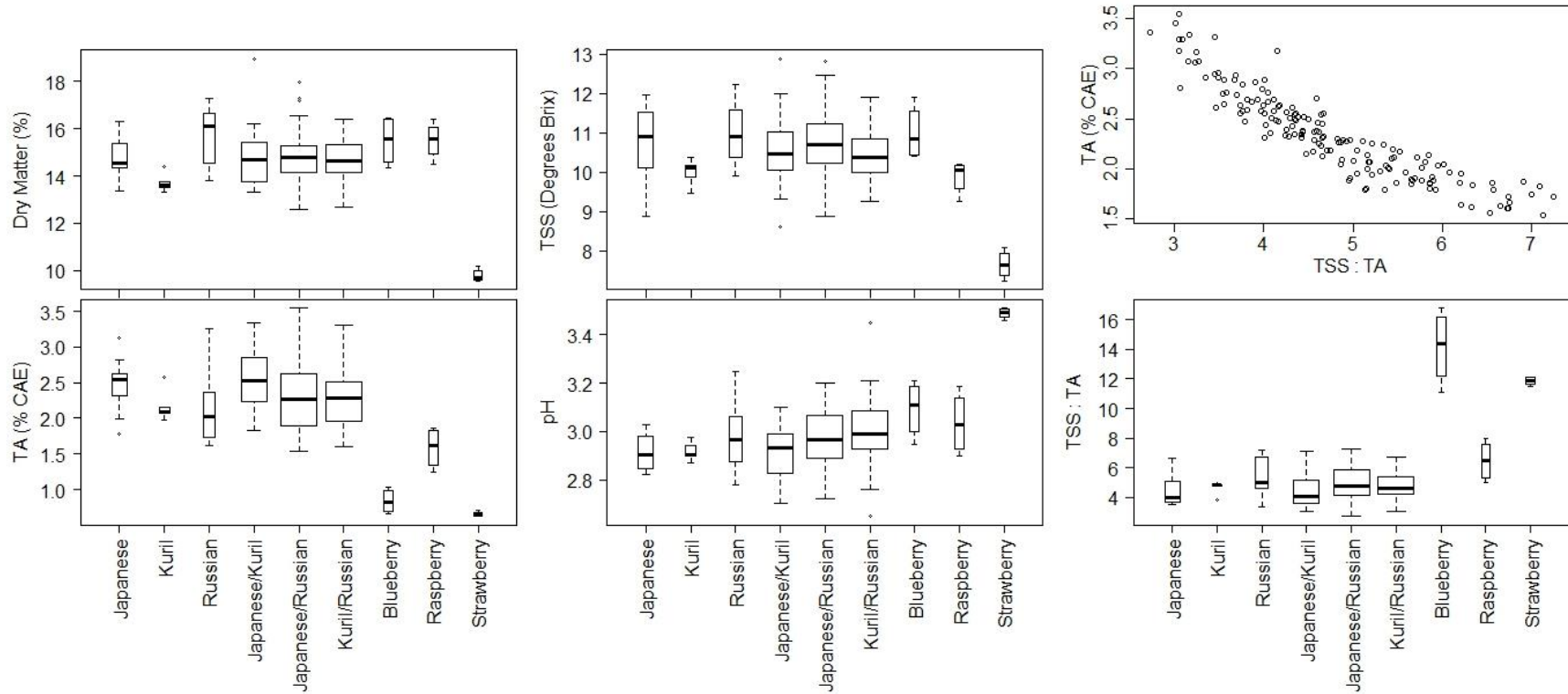
Figure 6.3. Foundation and Improved Germplasm: Fruit quality traits in blue honeysuckle and comparison crops evaluated in 2012/2013 in the Fraser Valley, BC, Canada and XY plot of two key fruit quality traits (TSS – total soluble solids, TA – titratable acidity, CAE – citric acid equivalents, boxplot widths are proportional to the square root of the sample size for each group).

Table 6.7. Foundation and Improved Germplasm: Fruit quality traits in blue honeysuckle in 2012/2013 in Chilliwack, BC, Canada (TSS – total soluble solids, TA – titratable acidity, CAE – citric acid equivalents).

		Japanese	Kuril	Russian	Japanese/ Kuril	Japanese/ Russian	Kuril/ Russian	Blue-berry	Rasp-berry	Straw-berry
Dry Matter (%)	Average	14.8	13.6	15.1	14.4	14.7	14.6	15.5	15.5	9.8
	Median	14.8	13.5	15.2	14.3	14.6	14.6	15.6	15.6	9.7
	Minimum	13.4	13.3	13.8	13.0	13.0	12.4	14.4	14.5	9.6
	Maximum	16.2	13.9	15.9	16.9	17.5	16.2	16.4	16.4	10.2
	Range	2.8	0.6	2.1	3.9	4.4	3.8	2.1	1.9	0.6
TSS (%)	Average	10.68	9.97	10.93	10.46	10.62	10.56	10.99	9.88	7.65
	Median	10.88	10.20	10.90	10.38	10.49	10.50	10.83	10.04	7.64
	Minimum	8.88	9.28	9.90	8.88	8.52	8.73	10.39	9.27	7.23
	Maximum	11.84	10.33	11.83	12.87	12.90	12.08	11.89	10.18	8.07
	Range	2.96	1.05	1.93	3.98	4.38	3.36	1.50	0.92	0.84
TA (% CAE)	Average	2.48	2.19	2.15	2.49	2.45	2.16	0.83	1.58	0.65
	Median	2.55	2.15	2.02	2.49	2.38	2.14	0.82	1.61	0.64
	Minimum	1.78	1.96	1.62	1.61	1.60	1.53	0.66	1.25	0.62
	Maximum	3.14	2.57	3.25	3.36	3.54	2.89	1.03	1.86	0.70
	Range	1.36	0.61	1.63	1.75	1.94	1.36	0.36	0.61	0.08
pH	Average	2.92	2.95	2.98	2.93	2.96	3.03	3.09	3.03	3.49
	Median	2.90	2.93	2.97	2.93	2.97	3.04	3.11	3.03	3.49
	Minimum	2.82	2.91	2.78	2.71	2.79	2.65	2.95	2.90	3.46
	Maximum	3.01	2.99	3.25	3.16	3.18	3.45	3.21	3.18	3.51
	Range	0.19	0.08	0.47	0.45	0.39	0.80	0.26	0.29	0.05
TSS:TA	Average	4.50	4.60	5.35	4.42	4.55	5.09	14.16	6.48	11.86
	Median	3.98	4.79	5.00	4.17	4.49	4.96	14.40	6.47	11.90
	Minimum	3.52	3.78	3.35	2.73	2.91	3.48	11.08	5.01	11.49
	Maximum	6.62	4.89	7.23	7.09	7.04	6.87	16.76	7.98	12.14
	Range	3.10	1.11	3.88	4.37	4.13	3.39	5.69	2.96	0.65

(3.39), followed by the Japanese/Russian (4.13) and then the Japanese/Kuril group (4.37).

For DM and TSS, the ranges for each improved group were larger than for any of the foundation groups on their own. For TA and TSS:TA, the range for the Kuril/Russian group was intermediate between the low and high ranges in the Kuril and Russian groups, respectively, though closer to the latter. Similarly, the range in pH for the Japanese/Russian group was intermediate between the low Japanese and high Russian ranges. Therefore, the overall ranges in DM (5.1%), TSS (4.4%), TA (2.01%) and pH (0.80) were the same as the ranges across the improved germplasm but larger than across the foundation germplasm (2.9%, 2.9%, 1.63% and 0.47) as the highest and lowest extremes were found in improved groups in each case. In contrast, the overall range for TSS:TA (4.50) was greater than across the improved germplasm (4.36) or foundation germplasm (3.88) as the highest and lowest genotypes were observed in the Russian and Japanese/Kuril groups, respectively.

Therefore, the absolute range of each variable was broader in the Japanese/Kuril group than in either the Japanese or Kuril foundation groups, and the upper and lower extremes completely overlapped the foundation group extremes. Correspondingly, the absolute range of each variable, except for pH, was broader for the Japanese/Russian group than either parent group. For pH, there was a broader range in the Russian but not the Japanese group. The Japanese/Russian group completely overlapped its parent groups for DM, TSS and TA, but completely overlapped only the Japanese group for pH and TSS:TA, overlapping neither Russian extreme for the former and only the lower extreme for the latter. The absolute ranges in DM, TSS and pH were broader for the Kuril/Russian group than either parent group and overlapped their extremes. For TA and TSS:TA, the ranges were broader and narrower than the Kuril and Russian groups, respectively. Consequently, the Kuril/Russian group overlapped the lower extremes of both parent groups and the upper extreme of only the Kuril group for TA, whereas it only overlapped the Kuril group extremes for TSS:TA.

For TSS and pH, H^2 was moderate, but it was high for DM, TA and TSS:TA across the foundation and improved germplasm combined and separate (**Table 6.8**). Within foundation groups, H^2 for all traits was moderate to high in the Japanese group; negligible in the Kuril group, excepting TA and TSS:TA for which it was high; and negligible in the Russian group, excepting TA and pH for which it was moderate and low, respectively. Similarly, within the improved germplasm, H^2 was moderate to very high in the Japanese/Kuril and Japanese/Russian groups but

Table 6.8. Foundation and Improved Germplasm: Heritability estimates for fruit quality traits for blue honeysuckle in 2012/2013 in Chilliwack, BC, Canada (H^2 – broad-sense heritability calculated from linear mixed model regression, h^2 – narrow-sense heritability calculated from mid-parent regression on phenotypic averages[1]).

	Dry Matter (%)		Total Soluble Solids (%)		Titratable Acidity (% Citric Acid Equivalents)		pH		Total Soluble Solids:Titratable Acidity	
	H^2	h^2	H^2	h^2	H^2	h^2	H^2	h^2	H^2	h^2
All Germplasm	0.74	-	0.51	-	0.89	-	0.66	-	0.87	-
All Foundation	0.82	-	0.53	-	0.88	-	0.69	-	0.78	-
Japanese	0.82	-	0.60	-	0.87	-	0.71	-	0.79	-
Kuril	0.09	-	0.00	-	0.83	-	0.05	-	0.71	-
Russian	0.05	-	0.07	-	0.51	-	0.47	-	0.13	-
All Improved	0.72	0.23	0.51	0.33	0.88	0.12	0.65	0.13	0.88	0.20
Japanese/Kuril	0.88	0.06	0.53	0.37	0.91	0.24	0.66	0.18	0.92	0.41
Japanese/Russian	0.73	0.41	0.56	0.41	0.90	0.04	0.67	0.06	0.90	0.11
Kuril/Russian	0.56	0.00	0.40	0.04	0.79	0.11	0.52	0.11	0.82	0.20

[1]Different regression models were used to calculate H^2 and h^2 heritability estimates, so these measures are not directly comparable.

low to high in the Kuril/Russian group. In comparison, h^2 was low for DM and TSS across the improved germplasm and negligible otherwise. Within improved groups, h^2 was low for TSS and TA and moderate for TSS:TA in the Japanese/Kuril group, moderate for DM and TSS in the Japanese/Russian group and low for TSS:TA in the Kuril/Russian group.

Across the foundation and improved germplasm combined and separate, H^2 for DM, TA and TSS:TA was higher than for pH, which was somewhat higher than for TSS. The same characteristic pattern was seen within improved groups, but the differences between variables were even more pronounced. H^2 ranged from very high for TA and TSS:TA in the Japanese/Kuril group to low for TSS in the Kuril/Russian group. Within the foundation germplasm, this general trend was seen in the Japanese group, but H^2 in the Kuril and Russian groups was not as clearly delineated: In the Kuril group, H^2 was high for TA and TSS:TA, as expected, but it was negligible for DM, TSS and pH. In the Russian group, H^2 was negligible for DM, TSS and TSS:TA while being moderate and low for TA and pH, respectively. Therefore, relative differences in H^2 between FQ traits across the germplasm were not reflected in the Kuril and Russian groups on their own as they were in the Japanese and improved groups on their own.

In the foundation germplasm, only the Japanese group had considerable H^2 for DM and TSS, the Japanese and Russian groups for pH, and the Japanese and Kuril groups for TSS:TA. In contrast, H^2 for TA was considerable in all three foundation groups. In the improved germplasm, H^2 for DM and TSS:TA was higher in the Japanese/Kuril than the Japanese/Russian group, which was higher than in the Kuril/Russian group. H^2 for TA was almost as high in the Japanese/Russian group as in the Japanese/Kuril group, but it was considerably lower in the Kuril/Russian group. H^2 for TSS and pH in the Japanese/Russian group was slightly higher and considerably lower than in the Japanese/Kuril and Kuril/Russian groups, respectively.

In the Japanese/Kuril group, H^2 was intermediate between the Japanese and Kuril groups for TSS and pH but higher than either for DM, TA and TSS:TA. In the Japanese/Russian group, H^2 was intermediate between the Japanese and Russian groups for DM, TSS and pH though higher than either group for TA and TSS:TA. In the Kuril/Russian group, H^2 was intermediate between the Kuril and Russian groups for TA while higher than either group for DM, TSS, pH and TSS:TA.

From another perspective, H^2 for DM was intermediate between parent groups in the Japanese/Russian group and higher in the Japanese/Kuril and Kuril/Russian groups. H^2 for TSS and pH was intermediate in the Japanese/Kuril and Japanese/Russian groups and higher in the

Kuril/Russian group. H^2 for TA was intermediate in the Kuril/Russian group and higher for the Japanese/Kuril and Japanese/Russian groups. For TSS:TA, H^2 was higher in all three improved groups. In contrast, across the improved germplasm, h^2 was higher for TSS than for DM and negligible for the other traits. Further, h^2 was only substantial for DM and TA in the Japanese/Kuril group, for TSS in the Japanese/Kuril and Japanese/Russian groups and for TSS:TA in the Japanese/Kuril and Kuril/Russian groups. For pH, h^2 was not substantial in any group.

6.2.3.3 Improved Japanese/Kuril Germplasm

The Japanese/Kuril group ranged in DM from 13.0-16.9%, TSS from 8.9-12.9%, TA from 1.61-3.36%, pH from 2.71-3.16 and TSS:TA from 2.73-7.09 (**Figure 6.3**; **Table 6.7**). The distributions of observations for DM, TA, pH and TSS:TA were similar to those of the Japanese group, while they were intermediate between the Japanese and Kuril groups for TSS. For DM and TA, there were more high than low transgressive segregants and parent types and a very small number of intermediates (**Figure 6.4**; **Appendix D.9**). TSS showed very little transgressive segregation of either type, but there were more high- than low-parent types and mostly intermediates. For pH, there was approximately the same number of high and low transgressive segregants but noticeably fewer high-parent types compared to low-parent types with nearly half intermediates. TSS:TA demonstrated a far greater number of low than high transgressive segregants and parent types and a quarter were intermediates. In summary, there was heavy skew toward high transgressive segregants and high-parent types for DM and TA, some skew toward high-parent types for TSS, a slight skew toward low-parent types for pH and a strong skew toward low transgressive segregants and low-parent types for TSS:TA. Therefore, the Japanese/Kuril group showed a high degree of additive gene action for TSS with a low degree of transgressive segregation overall but with dominance of the higher TSS contributed by the Japanese group. TSS:TA and pH demonstrated moderate proportions of additive gene action with dominance and overdominance of lower Japanese TSS:TA. DM and TA showed low proportions of additive gene action, resulting in both dominance and overdominance of higher Japanese levels.

6.2.3.4 Improved Japanese/Russian Germplasm

The Japanese/Russian group ranged in DM from 13.0-17.5%, TSS from 8.5-12.9%, TA from 1.60-3.54%, pH from 2.79-3.18 and TSS:TA from 2.91-7.04 (**Figure 6.3**; **Table 6.7**). The
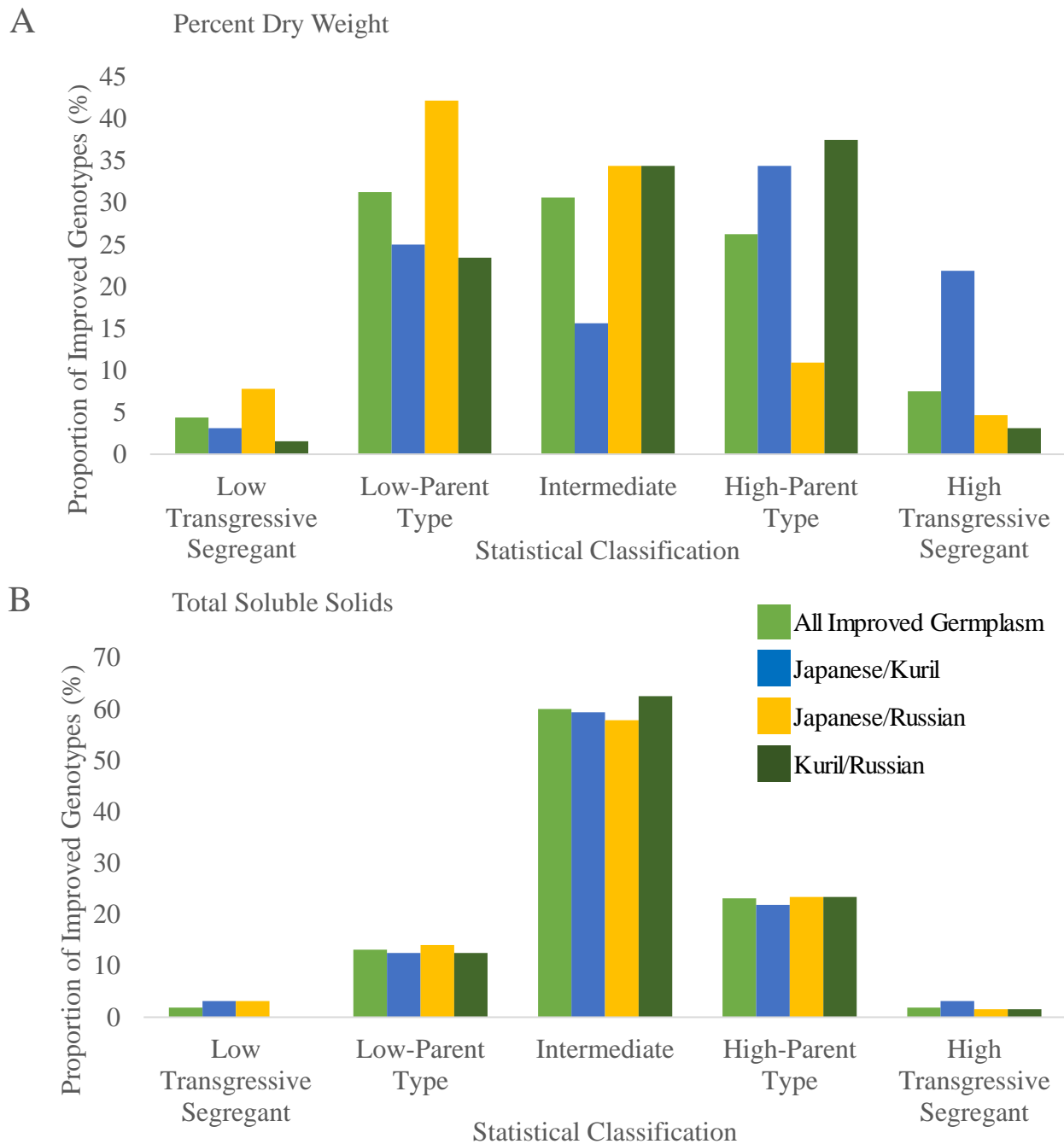
Figure 6.4. Improved Germplasm: Statistical classification of blue honeysuckle hybrids compared to their parent genotypes for fruit quality in 2012/2013 in Chilliwack, BC, Canada. (A) Dry matter (B) Total soluble solids (C) Titratable acidity (D) pH (E) Total soluble solids:titratable acidity.
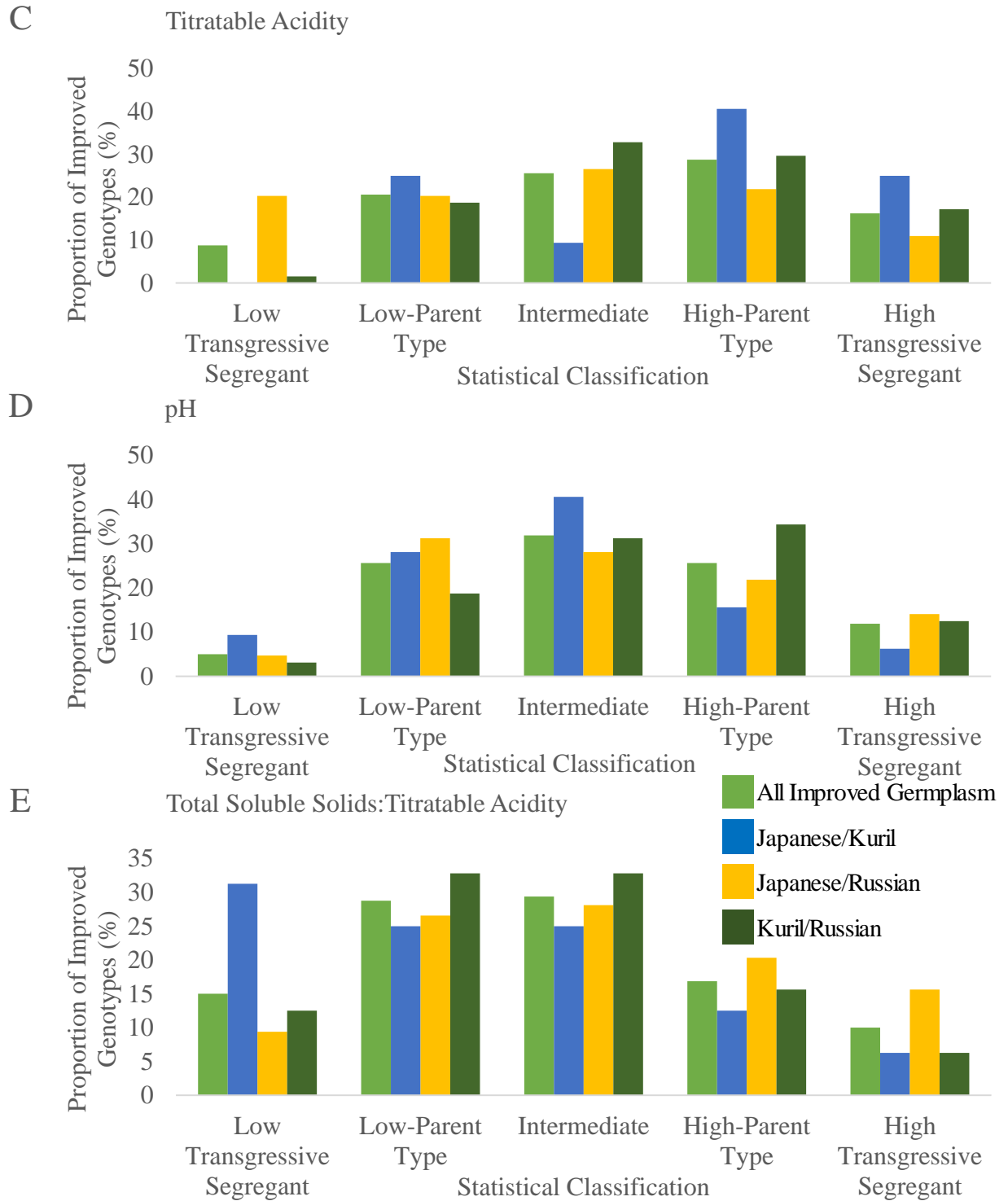
Figure 6.4. Continued. Improved Germplasm: Statistical classification of blue honeysuckle hybrids compared to their parent genotypes for fruit quality in 2012/2013 in Chilliwack, BC, Canada. (A) Dry matter (B) Total soluble solids (C) Titratable acidity (D) pH (E) Total soluble solids:titratable acidity.

distribution of observations for each variable was typically intermediate between the Japanese and Russian groups. For DM, there were only slightly more low than high transgressive segregants but far more low than high-parent types, leaving more than a third as intermediates. TSS:TA and pH showed slightly more high than low transgressive segregants but slightly more low-parent types than high with more than a quarter intermediates. TSS showed little transgressive segregation of any type, but there were more high-parent than low-parent types and mostly intermediates. TA showed twice as many low transgressive segregants as high, a similar abundance of low- and high-parent types and over a quarter intermediates (**Figure 6.4**; **Appendix D.9**). Overall, there was skew toward low-parent types for DM, pH and TSS:TA with some skew toward low transgressive segregants for DM and, contrastingly, high transgressive segregants for pH and TSS:TA. For TSS and TA, there was some skew toward high-parent types and low transgressive segregants, respectively. Therefore, the Japanese/Russian group showed a high proportion of additive gene action for TSS, a low degree of transgressive segregation but dominance of higher Russian TSS. Though all other variables showed moderate additive gene action, they had contrasting trends in dominance and overdominance: pH and TSS:TA showed dominance of low Japanese levels and contrasting overdominance of high Russian values; however, TA showed little skew in dominance but noticeable overdominance of lower Japanese levels, whereas DM showed little skew in overdominance but considerable dominance of the lower Japanese genetics.

6.2.3.5 Improved Kuril/Russian Germplasm

The Kuril/Russian group ranged in DM from 12.4-16.2%, TSS from 8.7-12.1%, TA from 1.53-2.89%, pH from 2.65-3.45 and TSS:TA from 3.48-6.87 (**Figure 6.3**; **Table 6.7**). The distributions of observations for DM, TSS and TSS:TA were intermediate between the Kuril and Russian groups, whereas they were skewed toward higher values for TA and pH. For DM and TSS, there was little transgressive segregation, but there were more high- than low-parent types; there were more than a third and almost two thirds intermediates, respectively. For TA and pH, there were more high than low transgressive segregants and parent types, leaving approximately a third as intermediates. In contrast, for TSS:TA, there were twice as many low transgressive segregants and low-parent types as high with a third intermediate types (**Figure 6.4**; **Appendix D.9**). In summary, there was a slight skew toward high-parent types for DM and TSS and a heavy skew toward high transgressive segregants and high-parent types for TA and pH, while there was

some skew toward low transgressive segregants and low-parent types for TSS:TA. Therefore, the Kuril/Russian group showed a high proportion of additive gene action for TSS and a low degree of transgressive segregation, with dominance of the higher Russian group. As for the Japanese/Russian group, while all other variables showed moderate degree of additive gene action, there was variability in patterns of dominance and overdominance. TA and pH showed dominance and overdominance of the higher Russian genetics. DM showed only dominance of the higher Russian values. In contrast, TSS:TA showed dominance and overdominance of the lower Kuril levels.

6.2.3.6 Mode of Gene Action across Improved Germplasm Groups

Across the improved germplasm, the total proportion of intermediates was highest for TSS, being half as prevalent for the other four traits (**Figure 6.4**; **Appendix D.9**). There were more intermediates in the Japanese/Russian and Kuril/Russian groups than the Japanese/Kuril group for DM and TA, but the opposite was seen for pH. Proportions were very similar across the improved groups for TSS and TSS:TA. Overall, in the Japanese/Kuril group, the proportion of intermediates was low for DM and TA, moderate for TSS:TA and high for TSS and pH. In the Japanese/Russian and Kuril/Russian groups, frequency of intermediates was moderate for all variables except TSS for which it was high.

Averaged across all groups, total incidence of transgressive segregation was higher for TA and TSS:TA than for DM and pH, whereas it was very low for TSS. For DM and TSS:TA, total transgressive segregation was more prevalent for the Japanese/Kuril group than the Japanese/Russian group, being lower still for the Kuril/Russian group. All improved groups had low degrees of transgressive segregation for TSS and moderate proportions for pH, but the Japanese/Kuril and Kuril/Russian groups had less transgressive segregation for TA than the Japanese/Russian group. In summary, total transgressive segregation was highest for DM and TSS:TA while more moderate for TA and pH in the Japanese/Kuril group. It was highest for TA and more moderate for DM, pH and TSS:TA in the Japanese/Russian group. However, it was moderate for TA, pH and TSS:TA but considerably lower for DM in the Kuril/Russian group. Across all three groups, total transgressive segregation was very low for TSS.

FQ traits combined in different ways, depending on the combination of foundation groups. The Japanese/Kuril group was skewed toward high-parent types for DM, TSS and TA as well as

high transgressive segregants for DM and TA but toward both low transgressive segregants and low-parent types for pH and TSS:TA. The Japanese/Russian group was skewed toward low-parent types and, contrastingly, high transgressive segregants for DM, pH and TSS:TA but toward high-parent types for TSS and low transgressive segregants for TA. The Kuril/Russian group was skewed toward high-parent types for DM, TSS, TA and pH and toward high transgressive segregants for the latter two variables, only tending toward both low-parent types and low transgressive segregants for TSS:TA. For context, DM and TSS compared similarly across the foundation germplasm, being higher in the Russian than the Japanese, being lowest for the Kuril group (**Section 6.2.2.1**). TSS:TA compared similar to pH, the Russian group being higher than the Kuril group, which was higher than the Japanese group. TA was unique, being higher for the Japanese group than the Russian group, which was higher than the Kuril group. For each FQ trait, there was higher H^2 in the Japanese/Kuril and Japanese/Russian groups, which both had a high H^2 Japanese parent, than in the Kuril/Russian group, which had two parent groups with lower or negligible H^2. Consequently, the three foundation groups combined in different ways for DM, TA, pH and TSS:TA, but they combined in a similar manner for TSS.

The Russian group had the highest DM, followed by the Japanese and then Kuril group, resulting in a more dissortive cross for the Kuril/Russian group than either the Japanese/Kuril or Japanese/Russian group. In the more assortive combinations of the Japanese group with either the Kuril or Russian group, hybrids resembled or transgressed the Japanese group. In the more dissortive combination of the Kuril and Russian groups, offspring were more often intermediate with a slight skew toward the higher Russian group but little transgressive segregation. Therefore, when the high H^2 Japanese parent was crossed with the negligible H^2 Kuril and Russian groups, the improved groups had higher H^2 than for crosses between the latter two foundation groups. Whether it was the higher (Japanese/Kuril) or lower (Japanese/Russian) DM parent, the Japanese group demonstrated dominance relating to its higher H^2, but overdominance was more apparent for the Japanese/Kuril group when the Japanese parent had both higher DM and H^2. Overall, dominance and overdominance were associated with relative comparisons in DM between foundation groups and differences in H^2.

The Russian group had higher average TSS than the Japanese group, which had higher average TSS than the Kuril group. Statistical comparison of parent genotypes suggested a slightly greater degree of dissortive mating for the Japanese/Russian group than the Kuril/Russian group,

whereas the Japanese/Kuril group was a relatively assortive combination. All three foundation groups combined similarly, resulting in mostly intermediates, very little transgressive segregation and a slight skew toward the foundation group with the higher TSS in each combination. In summary, there was dominance of higher Russian or Japanese TSS in all three improved groups, but little overdominance despite differences in H^2 between the foundation groups.

The Japanese group had higher TA than the Russian group for which the average was only slightly higher than for the Kuril group, making the Japanese/Kuril and Japanese/Russian crosses relatively more dissortive than the Kuril/Russian combination. The Japanese/Kuril group was skewed toward higher Japanese TA and high transgressive segregation. The Japanese/Russian group was not skewed toward higher Japanese TA, rather being skewed toward low transgressive segregation. The Kuril/Russian group had a slight skew toward the higher Russian group and high transgressive segregation. Therefore, high and intermediate TA of the Japanese and Russian groups showed dominance and overdominance over lower TA of the Kuril group. There was no observed dominance of relatively higher Japanese TA over the intermediate Russian group, but there was some overdominance of reduced TA in contrast to the other two improved groups.

Compared to the other FQ traits, differences in pH across foundation groups were much less distinct, and comparison of parent genotypes demonstrated a mixture of dissortive and assortive crosses within the improved germplasm. The Japanese/Kuril group was skewed toward lower Japanese pH and low transgressive segregation. The Japanese/Russian group was skewed toward high transgressive segregation beyond the high pH observed for the Japanese group, which contrasted with its greater proportion of low-parent types. The Kuril/Russian group was heavily skewed toward high Kuril pH with many high transgressive segregants as well. The dominance and overdominance of low pH in the Japanese/Kuril group was the converse of the dominance and overdominance of higher TA in the Japanese/Kuril group, which was expected since TA and pH are usually negatively correlated. Correspondingly, the Japanese/Russian group showed the opposite trend with overdominance toward low TA and high pH, as expected, but there was no clear pattern in dominance for TA and only slight dominance of low pH. Further, the Kuril/Russian group showed corresponding dominance and overdominance of both high TA and pH, which is contrary to the expectation for these negatively correlated traits. This may be related to the lower phenotypic correlation (**Section 6.2.3.7**) between pH and TA observed in the Kuril/Russian group than the other improved groups, which is reflective of a lower correlation in the Kuril group than

246

the other foundation groups. Low pH was dominant and overdominant over more intermediate pH between the Japanese and Kuril groups, while high pH was dominant and overdominant over the low pH between the Russian group and both the Japanese and Kuril groups. Therefore, dominance and overdominance of high and low pH over intermediate pH in assortive combinations contrasted with dominance of low and overdominance of high pH in a dissortive combination.

The Russian group had higher average TSS:TA than the Kuril group, which had higher average TSS:TA than the Japanese group, making the Japanese/Russian cross more dissortive than the Japanese/Kuril or Kuril/Russian crosses. All three groups were skewed toward low-parent types, but the assortive Japanese/Kuril and Kuril/Russian combinations were also skewed toward low transgressive segregation. In contrast, the dissortive Japanese/Russian group was skewed toward high transgressive segregation. Therefore, the contrasting dominance of low TSS:TA and overdominance of high TSS:TA for the Japanese/Russian group was related to dominance of high TSS and overdominance of low TA in this same group. Conversely, the dominance and overdominance of low TSS:TA in the Japanese/Kuril and Kuril/Russian groups demonstrated the greater importance of dominance and overdominance of high TA compared to dominance of high TSS. Overall, the low ratios in the Japanese group showed dominance and overdominance over the intermediate ratios in the Kuril group, while the intermediate ratios in the Kuril group showed dominance and overdominance over the high ratios in the Russian group. In contrast, the high and low ratios in the Russian and Japanese groups showed dominance and overdominance, respectively, in this more dissortive cross.

For comparison, in Russia's Altai krai, mixed-pollen hybrid populations between ssp. *altaica* and ssp. *kamtschatica* cultivars showed intermediate TSS to the two parental ssp., but higher TA and TSS:TA like ssp. *altaica* (Krisova et al 2012). Therefore, between these Russian ssp., prevalence of additive gene action in TSS concurred with the current findings across improved groups. Also, dominance of high TA concurred with the results in the Japanese/Kuril and Kuril/Russian groups but not Japanese/Russian group. However, dominance of high TSS:TA was contrary to observations in the current study.

6.2.3.7 Blueberry, Raspberry and Strawberry Compared to Improved Germplasm

For all FQ traits, the phenotypic ranges of the blueberry, raspberry and strawberry cultivars were restricted compared to each improved group (**Figure 6.3**; **Table 6.7**). For DM, the high and

low extremes for blueberry (14.4-16.4%) and raspberry (14.5-16.4%) were overlapped by each of the improved blue honeysuckle groups except for the Kuril/Russian group's upper extreme. The strawberry cultivars were restricted to a narrower range of far lower values (9.6-10.2%) than even the lowest observations in the improved germplasm. Overall, average DM for each improved group was only slightly lower than for blueberry and raspberry though several percent higher than strawberry. Similarly, for TSS, the high and low extremes for blueberry (10.4-11.9%) and raspberry (9.3-10.2%) were overlapped by the extremes of each of the improved groups, while the high and low extremes for strawberry were far lower (7.2-8.1%) than even the lowest observations in the improved germplasm. The average TSS for each improved group was slightly lower than blueberry and higher than raspberry and strawberry, by three percent for the latter.

For TA, the average for raspberry (1.58%) was lower than the lowest extreme in any improved blue honeysuckle group, but the upper extreme overlapped slightly with their lower extremes. The averages for blueberry (0.83%) and strawberry (0.65%) were far lower than even the lowest blue honeysuckle extreme. In contrast, the average raspberry pH (3.03) was the same as that of the Kuril/Russian group, and the average blueberry pH (3.09) was only slightly higher than for each of the improved groups. The ranges in both raspberry and blueberry ranges were completely overlapped by the range of each of the improved group. The strawberry average was higher than even the highest blue honeysuckle extreme.

The average blueberry TSS:TA (14.16) was approximately three times greater than that of any foundation or improved blue honeysuckle group. The lowest blueberry ratio (11.08) was twice the average of any blue honeysuckle group, whereas the highest ratio (16.76) was more than two times higher than the highest blue honeysuckle. Further, the raspberry average (6.48) was higher than that of any foundation or improved group; the low-end extreme (5.01) was on par with the average for the highest improved group (Kuril/Russian group); and the high-end extreme (7.98) was slightly higher than the highest blue honeysuckle. The strawberry average (11.86) was more than two times greater than the average for any foundation or improved blue honeysuckle group.

Parallel evaluations of improved germplasm seedling plots in Saskatchewan demonstrate important genetic progress for TSS and TA (Bors et al 2015). In 2012, 2013 and 2014, the average improved germplasm selection had 14.2, 15.8 and 16.4% TSS, respectively, and 2.17, 1.83 and 1.89% TA (tartaric acid equivalents), respectively, TSS ranging from 10 to more than 20% and

TA from approximately 1-4%. The range in TSS:TA for these selections varied from 4.97 to 19.71.

6.2.3.8 Correlations between Fruit Quality Traits

Across the foundation and improved germplasm, there were moderate and low positive correlations for DM with TSS and TSS:TA, respectively (**Table 6.9**). Also, there was a moderate positive correlation between TSS and TSS:TA and a corresponding high negative correlation between TA and TSS:TA (**Figure 6.3**), supporting evidence of a more important role for TA than TSS in determining TSS:TA (**Section 6.2.1.4**). Moreover, a moderate negative correlation between TA and pH resulted in a moderate positive correlation between pH and TSS:TA.

The strength, and sometimes direction, of these correlations varied across foundation and improved groups. The positive correlation between DM and TSS was low for the Japanese and Kuril/Russian groups, moderate for the Japanese/Kuril and Japanese/Russian groups and high for the Kuril and Russian groups. For DM and TSS:TA, the correlation was low and positive for the Kuril, Japanese/Russian and Kuril/Russian groups but, in contrast, moderate and negative for the Russian group and negligible for the Japanese group. Between TSS and TSS:TA, there were no correlations for any foundation group on its own but there were low to moderate positive correlations for the improved groups.

For TA and pH, the correlation was low for the Kuril and Kuril/Russian groups, moderate for the Japanese/Kuril and Japanese/Russian groups and high for the Japanese and Russian groups. Between TA and TSS:TA, correlations were high to very high within each foundation and improved group on its own. Similarly, between pH and TSS:TA, correlations were low for the Kuril/Russian group, very high for the Russian group and moderate for all other groups.

Corresponding with these phenotypic correlations, across the improved germplasm, hybrid/parent comparisons (i.e., correlations between statistical classifications of hybrid genotypes) showed a low positive correlation for DM and TSS (**Table 6.10**); moderate and high negative correlations for TA with pH and TSS:TA, respectively; and a corresponding moderate positive correlation for pH with TSS:TA. These correlations were seen in each improved group on its own and were of similar strength as the phenotypic correlations. There were some additional correlations between hybrid/parent comparisons in the Japanese/Kuril group on its own: low negative correlations between DM and TA and between TSS and TA not reflecting phenotypic

Table 6.9. Foundation and Improved Germplasm: Pearson's correlations between biochemical determinants of fruit quality for blue honeysuckle in 2012/2013 in Chilliwack, BC, Canada (only statistically significant correlations [$p < 0.05$] are shown, DM – dry matter, TSS – total soluble solids, TA – titratable acidity, CAE – citric acid equivalents).

		Group	r			Group	r
DM (%)	TSS (%)	All Germplasm	0.556	TA (% CAE)	pH	All Germplasm	*-0.552*
		Japanese	0.485			Japanese	*-0.780*
		Kuril	0.765			Kuril	*-0.495*
		Russian	0.897			Russian	*-0.890*
		Japanese/Kuril	0.612			Japanese/Kuril	*-0.673*
		Japanese/Russian	0.647			Japanese/Russian	*-0.528*
		Kuril/Russian	0.418			Kuril/Russian	*-0.475*
	TA (% CAE)	Russian	0.657		TSS:TA	All Germplasm	*-0.866*
	pH	Japanese	*-0.521*			Japanese	*-0.838*
		Kuril	*-0.354*			Kuril	*-0.962*
		Russian	*-0.753*			Russian	*-0.965*
	TSS:TA	All Germplasm	0.358			Japanese/Kuril	*-0.889*
		Kuril	0.318			Japanese/Russian	*-0.877*
		Russian	*-0.681*			Kuril/Russian	*-0.858*
		Japanese/Russian	0.395	pH	TSS:TA	All Germplasm	0.529
		Kuril/Russian	0.323			Japanese	0.669
TSS (%)	TA (% CAE)	Japanese	0.384			Kuril	0.536
		Russian	0.554			Russian	0.924
	pH	Japanese	*-0.399*			Japanese/Kuril	0.661
		Russian	*-0.616*			Japanese/Russian	0.504
	TSS:TA	All Germplasm	0.510			Kuril/Russian	0.459
		Russian	*-0.549*				
		Japanese/Kuril	0.501				
		Japanese/Russian	0.526				
		Kuril/Russian	0.369				

Table 6.10. Improved Germplasm: Rho correlations between statistical classifications of hybrid blue honeysuckle genotypes for biochemical determinations of fruit quality in 2012/2013 in Chilliwack, BC, Canada (only statistically significant correlations [p < 0.05] are shown, DM – dry matter, TSS – total soluble solids, TA – titratable acidity, CAE – citric acid equivalents).

		Group	r
DM (%)	TSS (%)	All Improved	0.483
		Japanese/Kuril	0.592
		Japanese/Russian	0.455
		Kuril/Russian	0.472
	TA (% CAE)	Japanese/Kuril	*-0.440*
	TSS:TA	Japanese/Kuril	0.555
TSS (%)	TA (% CAE)	Japanese/Kuril	*-0.330*
	TSS:TA	Japanese/Kuril	0.487
TA (% CAE)	pH	All Improved	*-0.593*
		Japanese/Kuril	*-0.591*
		Japanese/Russian	*-0.733*
		Kuril/Russian	*-0.537*
	TSS:TA	All Improved	*-0.818*
		Japanese/Kuril	*-0.872*
		Japanese/Russian	*-0.901*
		Kuril/Russian	*-0.673*
pH	TSS:TA	All Improved	0.610
		Japanese/Kuril	0.563
		Japanese/Russian	0.726
		Kuril/Russian	0.539

correlations; a moderate positive correlation between DM and TSS:TA, which contrasted with phenotypic correlations that were only seen for the Japanese/Russian and Kuril/Russian groups; and a low positive correlation between TSS and TSS:TA that reflected phenotypic correlations for all three improved groups.

These trends provide strong evidence of the importance of TA (and pH by correlation) in determining TSS:TA across the foundation and improved germplasm. Only the Russian foundation group had a correlation between TSS and TSS:TA, and this correlation was not very strong in any improved group. Conversely, the correlation between TA and TSS:TA was high to very high across the foundation and improved germplasm and within foundation and improved groups individually. The highest correlations in the improved germplasm were for the Japanese/Kuril and Japanese/Russian groups, perhaps relating to the greater degree of variability for TSS in the Japanese group and the fact that it was the only foundation group with substantial H^2 for this trait.

6.2.4   Potential Human Health Benefits of Improved Germplasm
6.2.4.1 Parent Genotype Contrasts for Improved Germplasm Families

For the Japanese/Kuril group, the Kuril parent had higher TP in a single family on a DW basis only, but for TAC and FRAP, the Kuril parent was higher for seven and eight families on a FW basis, respectively, and six and seven families on a DW basis (**Appendix D.8**). For the Japanese/Russian group, TAC was higher for the Japanese and Russian parent for two families each, but only on a DW basis as there were no differences on a FW basis. TAC and FRAP were higher for the Russian parent in ten and fifteen families on a FW basis and in six and fourteen families on a DW basis. For the Kuril/Russian group, TP was not statistically different for any family on either a FW or DW basis. However, the Russian parent had higher TAC for one family, on a FW basis only, and higher FRAP for twelve and four families on a FW and DW basis, respectively. Therefore, there were no clear contrasts between parent genotypes for TP, especially on a FW basis. For TAC and FRAP, the Kuril and Russian parents were more often higher than the Japanese parents, while the Russian parent was only statistically higher than the Kuril parent for FRAP. For both TAC and FRAP, the statistical differences between parent genotypes were more distinct on a FW than DW basis, the opposite being true for TP.

6.2.4.2 Absolute Range, Group Extremes and Heritability

The lowest TP (353.7/2,399.6 mg GAE/100 g FW/DW), TAC (0.75/5.28 mmol TE/100 g FW/DW) and FRAP (3.26/22.96 mmol AAE/100 g FW/DW) were all found in the Japanese/Kuril group, whereas the highest TP (853.9/6,073.2 mg GAE/100 g FW/DW), TAC (3.00/24.37 mmol TE/100 g FW/DW) and FRAP (10.67/70.86 mmol AAE/100 g FW/DW) were observed in the Japanese/Kuril, Kuril/Russian and Japanese/Russian groups, respectively (**Figure 6.5**; **Table 6.11; Table 6.12**). The low extremes of TP in the Japanese/Russian group (398.1/2,643.6 mg GAE/100 g FW/DW) and Kuril/Russian group (400.9/2,732.7 mg GAE/100 g FW/DW) were nearly as low compared to the Japanese/Kuril group, but the high extremes (735.3/5,778.9 and 737.0/5,629.6 mg GAE/100 g FW/DW, respectively) were lower by a wide margin. For TAC and FRAP, compared to the low extremes in the Japanese/Kuril group, the lowest Japanese/Russian genotype (1.10/5.28 mmol TE/100 g FW/DW and 3.76/25.67 mmol AAE/100 g FW/DW) was substantially higher and the lowest Kuril/Russian genotype (1.40/9.34 mmol TE/100 g FW/DW and 4.69/30.65 mmol AAE/100 g FW/DW) was even higher. For TAC, compared to the high extreme in the Kuril/Russian group, the highest Japanese/Kuril (2.90/23.00 mmol TE/100 g FW/DW) and Japanese/Russian genotypes (2.89/24.33 mmol TE/100 g FW/DW) were very similar. However, for FRAP, the highest Japanese/Kuril genotype (6.74/60.00 mmol AAE/100 g FW/DW) was considerably lower compared to the high extreme in the Japanese/Russian group, but the highest Kuril/Russian genotype (9.70/70.43 mmol AAE/100 g FW/DW) was nearly as high.

For TP, the Japanese/Russian and Kuril/Russian groups had similar absolute ranges on a FW basis (337.2 and 336.2 mg GAE/100 g FW, respectively), but the range was broader for the former (3,135.3 mg GAE/100 g DW) than the latter (2,897.0 mg GAE/100 g DW) on a DW basis. For TAC on a FW basis, the range was slightly greater in the Japanese/Russian group than the Kuril/Russian group and slightly greater still in the Japanese/Kuril group. On a DW basis, the range was intermediate in the Japanese/Russian group, with higher and lower ranges in the Japanese/Kuril and Kuril/Russian groups, respectively. For FRAP on a FW basis, the range was considerably greater in the Japanese/Russian group than the Kuril/Russian group, the range in the Japanese/Kuril group being narrower still. These differences were not as distinct on a DW basis.

253
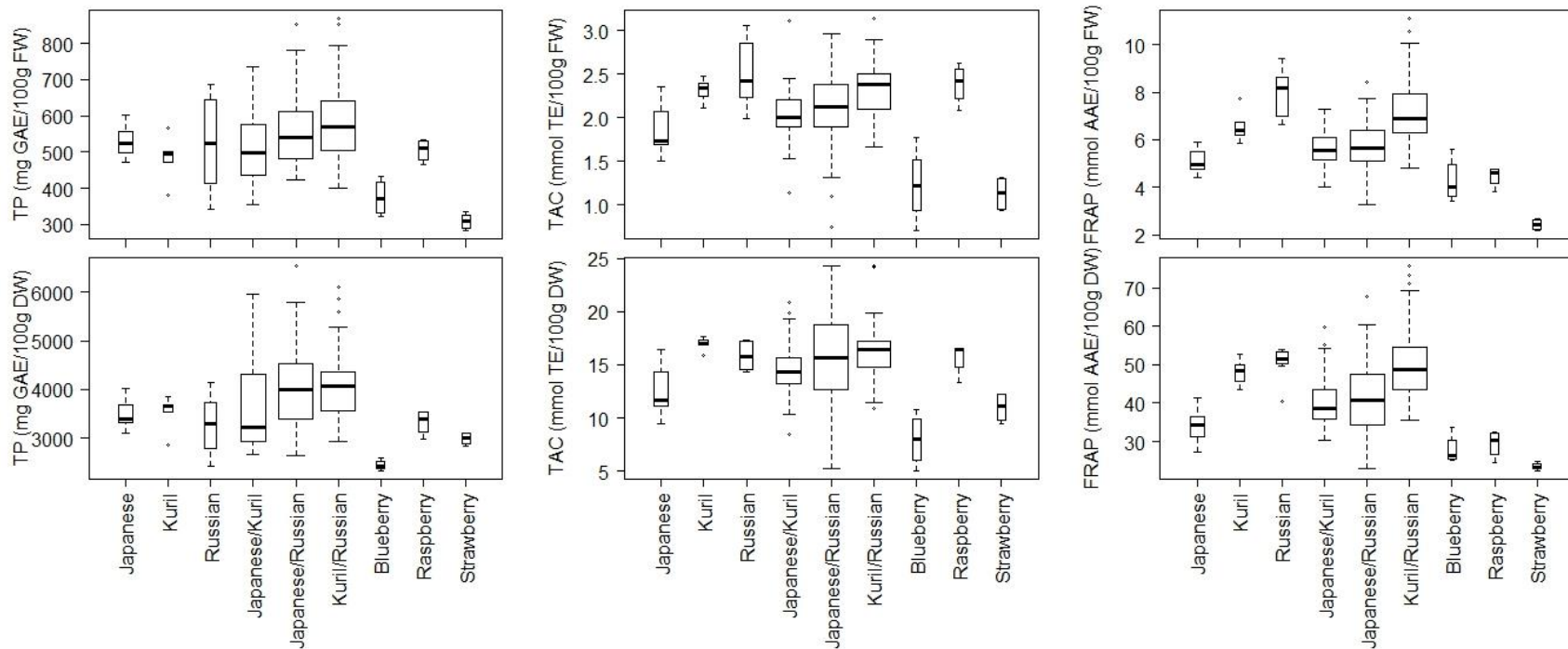
Figure 6.5. Foundation and Improved Germplasm: Nutritional content traits in blue honeysuckle and comparison crops evaluated in 2012/2013 in Chilliwack, BC, Canada (FW – fresh weight, DW – dry weight, TP – total phenolics, GAE – gallic acid equivalents, TAC – Trolox Antioxidant Capacity, TE – Trolox equivalents, FRAP – ferric reducing antioxidant potential, AAE – ascorbic acid equivalents, boxplot widths are proportional to the square root of the sample size for each group).

Table 6.11. Foundation and Improved Germplasm: Total phenolics and antioxidant activity in blue honeysuckle and comparison crops in 2012/2013 in Chilliwack, BC, Canada (FW – fresh weight, DW – dry weight, GAE – gallic acid equivalents, TAC – Trolox Antioxidant Capacity, TE – Trolox equivalents, FRAP – ferric reducing antioxidant potential, AAE – ascorbic acid equivalents).

	Group	Japanese	Kuril	Russian	Japanese/ Kuril	Japanese/ Russian	Kuril/ Russian	Blue-berry	Rasp-berry	Straw-berry
					Total Phenolics					
mg GAE/ 100 g FW	Average	518.8	461.4	466.2	499.1	552.0	561.0	373.7	505.2	308.6
	Median	525.3	470.5	473.9	464.8	545.6	556.6	371.0	511.5	308.3
	Minimum	471.4	382.4	340.5	353.7	398.1	400.9	321.0	464.5	282.7
	Maximum	559.5	535.9	573.2	853.9	735.3	737.0	431.9	533.2	335.1
	Range	88.1	153.4	232.8	500.3	337.2	336.2	110.9	68.7	52.4
mg GAE/ 100 g DW	Average	3449.1	3369.7	2977.4	3584.0	3912.8	4047.7	2444.7	3324.7	2992.6
	Median	3399.5	3507.9	2994.0	3139.8	3775.7	4100.1	2422.5	3396.0	3008.5
	Minimum	3045.5	2864.7	2431.9	2399.6	2643.6	2732.7	2339.6	2970.8	2842.7
	Maximum	3950.9	3683.2	3449.0	6073.2	5778.9	5629.6	2594.3	3535.9	3110.5
	Range	905.4	818.5	1017.2	3673.6	3135.3	2897.0	254.7	565.1	267.9

Table 6.11. Continued. Foundation and Improved Germplasm: Total phenolics and antioxidant capacity in blue honeysuckle and comparison crops in 2012/2013 in Chilliwack, BC, Canada (FW – fresh weight, DW – dry weight, GAE – gallic acid equivalents, TAC – Trolox Antioxidant Capacity, TE – Trolox equivalents, FRAP – ferric reducing antioxidant potential, AAE – ascorbic acid equivalents).

	Group	Japanese	Kuril	Russian	Japanese/ Kuril	Japanese/ Russian	Kuril/ Russian	Blue-berry	Rasp-berry	Straw-berry
				Trolox Antioxidant Capacity						
mmol TE/100 g FW at 5 min	Average	1.84	2.28	2.36	2.05	2.06	2.28	1.23	2.39	1.13
	Median	1.73	2.28	2.31	2.07	2.04	2.32	1.22	2.42	1.13
	Minimum	1.50	2.11	1.99	0.75	1.10	1.40	0.70	2.09	0.94
	Maximum	2.31	2.41	2.71	2.90	2.89	3.00	1.77	2.63	1.31
	Range	0.80	0.30	0.72	2.15	1.79	1.60	1.07	0.54	0.37
mmol TE/100 g DW at 5 min	Average	12.38	16.76	15.22	14.63	14.60	16.55	7.97	15.68	10.99
	Median	11.69	16.84	15.27	14.29	15.00	16.37	8.05	16.39	11.16
	Minimum	9.46	15.83	13.85	5.28	7.31	9.34	5.06	13.38	9.40
	Maximum	16.15	17.52	16.29	23.00	24.33	24.37	10.73	16.57	12.23
				Ferric Reducing Antioxidant Potential						
mmol AAE/100 g FW at 4 min	Average	5.09	6.43	7.65	5.40	5.99	6.66	4.28	4.46	2.43
	Median	4.95	6.42	7.53	5.40	5.88	6.53	4.03	4.63	2.44
	Minimum	4.40	5.82	6.51	3.26	3.76	4.69	3.44	3.83	2.17
	Maximum	5.91	7.35	8.99	6.74	10.67	9.70	5.61	4.77	2.67
	Range	1.51	1.52	2.48	3.49	6.91	5.00	2.17	0.94	0.50
mmol AAE/100 g DW at 4 min	Average	34.06	47.07	49.42	38.72	42.54	47.96	27.88	29.41	23.56
	Median	34.21	47.51	50.44	37.81	41.73	47.98	26.38	30.38	23.42
	Minimum	27.38	43.61	39.67	22.96	25.67	30.65	25.05	24.45	22.50
	Maximum	40.48	50.77	53.99	60.00	70.86	70.43	33.71	32.43	24.91
	Range	13.10	7.17	14.32	37.04	45.19	39.78	8.66	7.98	2.41

As for most FQ traits (**Section 6.2.3.1**), the overall ranges for TP (500.2/3,673.6 mg GAE/100 g FW/DW), TAC (2.25/19.09 mmol TE/100 g FW/DW) and FRAP (7.41/47.90 mmol AAE/100 g FW/DW) were the same as the ranges across the improved germplasm but larger than across the foundation germplasm. This was because the highest and lowest extremes for TP were both found in the Japanese/Kuril group, for TAC were in the Japanese/Kuril and Kuril/Russian groups, respectively, and for FRAP were in the Japanese/Kuril and Japanese/Russian groups, respectively.

For TP, H^2 and h^2 were negligible across the foundation and improved germplasm combined and separate as well as within each group on its own (**Table 6.12**). In contrast to TP, trends in H^2 for TAC and FRAP were clearer on a FW basis than DW. For TAC, H^2 was low across the foundation and improved germplasm combined and the improved germplasm on its own but was negligible for the foundation germplasm on its own. For FRAP, H^2 was moderate across the foundation and improved germplasm combined and separate. Each foundation group on its own had negligible H^2 for TAC and FRAP, as did the Japanese/Kuril group, but H^2 was low for the Japanese/Russian and Kuril/Russian groups on their own. Consequently, h^2 was negligible across the improved groups combined and separate for TAC but low across the improved germplasm for FRAP. These findings provide evidence contrary to initial speculation in Corvallis that TP and AOA may show substantial H^2 (Thompson and Chaovanalikit 2003).

6.2.4.3 Improved Japanese/Kuril Germplasm

For the Japanese/Kuril group, TP ranged from 353.7-853.9 mg GAE/100 g FW and 2,399.6-6,073.2 mg GAE/100 g DW (**Figure 6.5**; **Table 6.11**). TAC ranged from 0.75-2.90 mmol TE/100 g FW and 5.28-23.00 mmol TE/100 g DW. FRAP ranged from 3.26-6.74 mmol AAE/100 g FW and 22.96-60.00 mmol AAE/100 g DW. The distribution of observations for TP was bimodal, as was seen for both the Japanese and Kuril foundation groups. However, for TAC and FRAP, distributions were intermediate between the high Kuril and low Japanese foundation groups. FW and DW calculations of TP and TAC compared correspondingly between the Japanese/Kuril group and the Japanese and Kuril groups, completely overlapping the extremes of both parent groups. For FRAP, the overlap was more complete on a DW basis.

For TP, there were more low than high transgressive segregants and parent types, less than half being intermediates on a FW basis and very few on a DW basis (**Figure 6.6**; **Appendix D.11**). For TAC, there were many low transgressive segregants and no high transgressive segregants, but

Table 6.12. Foundation and Improved Germplasm: Heritability estimates for nutritional content traits for blue honeysuckle in 2012/2013 in Chilliwack, BC, Canada (H^2 – broad-sense heritability calculated from linear mixed model regression, h^2 – narrow-sense heritability calculated from mid-parent regression on phenotypic averages[1], FW – fresh weight, DW – dry weight, GAE – gallic acid equivalents, TE – Trolox equivalents, AAE -ascorbic acid equivalents).

	Total Phenolics				Trolox Antioxidant Capacity				Ferric Reducing Antioxidant Potential			
	mg GAE/100 g FW		mg GAE/100 g DW		mmol TE/100 g FW at 5 minutes		mmol TE/100 g DW at 5 minutes		mmol AAE/100 g FW at 4 minutes		mmol AAE/100 g DW at 4 minutes	
	H^2	h^2	H^2	h^2	H^2	h^2	H^2	h^2	H^2	h^2	H^2	h^2
All Germplasm	0.21	-	0.21	-	0.38	-	0.29	-	0.54	-	0.38	-
All Foundation	0.01	-	0.01	-	0.28	-	0.36	-	0.55	-	0.64	-
Japanese	0.00	-	0.02	-	0.19	-	0.29	-	0.16	-	0.32	-
Kuril	0.01	-	0.00	-	0.03	-	0.02	-	0.05	-	0.02	-
Russian	0.01	-	0.01	-	0.02	-	0.03	-	0.10	-	0.20	-
All Improved	0.28	0.00	0.24	0.03	0.40	0.08	0.27	0.03	0.53	0.26	0.35	0.23
Japanese/Kuril	0.25	0.00	0.30	0.02	0.27	0.00	0.17	0.00	0.28	0.00	0.26	0.04
Japanese/Russian	0.30	0.00	0.21	0.09	0.38	0.00	0.28	0.00	0.42	0.00	0.27	0.01
Kuril/Russian	0.22	0.00	0.15	0.00	0.47	0.01	0.37	0.04	0.39	0.00	0.28	0.06

[1]Different regression models were used to calculate H^2 and h^2 heritability estimates, so these measures are not directly comparable.
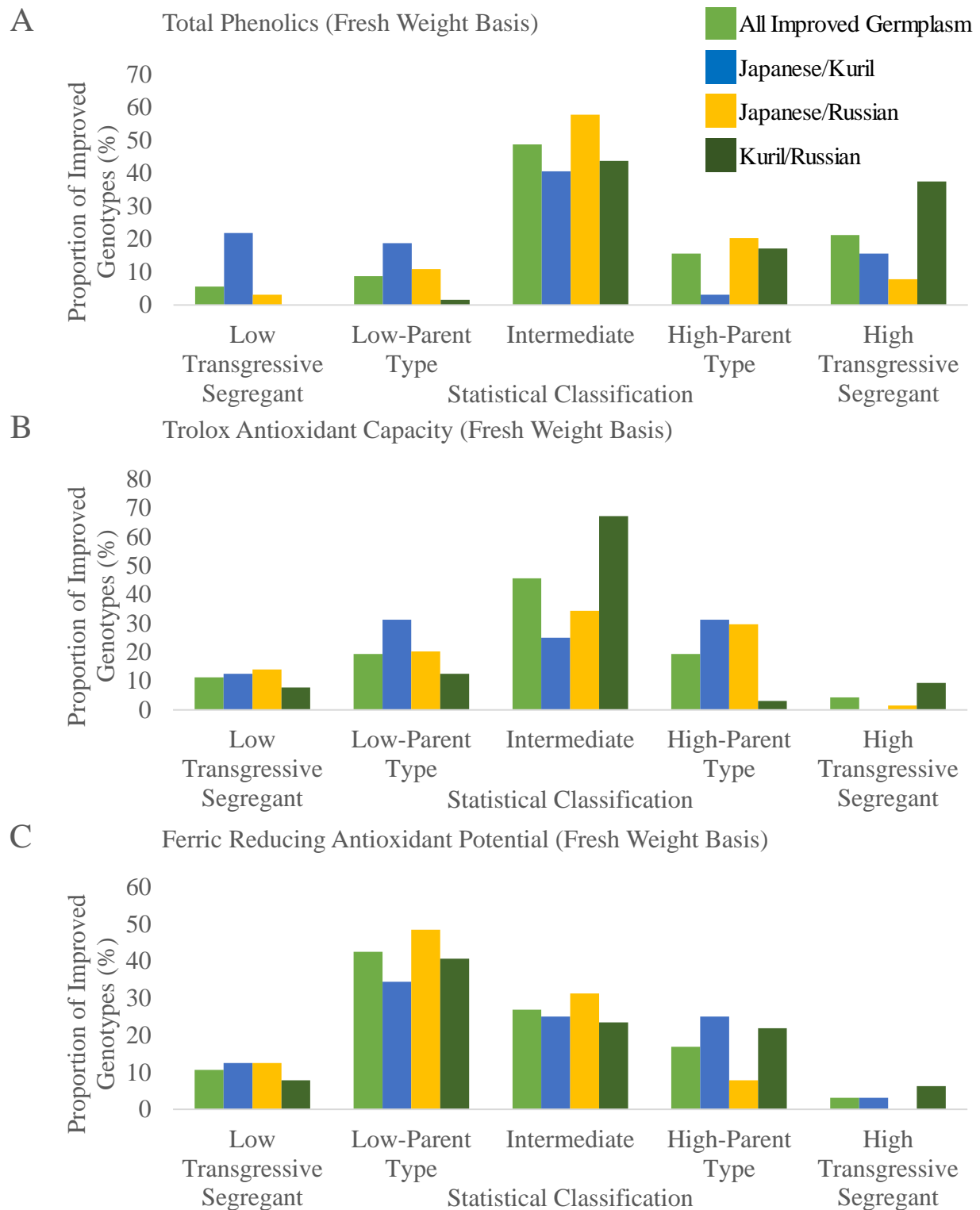
Figure 6.6. Improved Germplasm: Statistical classification of blue honeysuckle hybrids compared to parent genotypes for nutritional content traits in 2012/2013. (A) Total phenolics (B) Trolox equivalence antioxidant capacity (C) Ferric reducing antioxidant potential.

there were equal proportions of low- and high-parent types. For FRAP, there were more low than high transgressive segregants and parent types, as for TP. For both TAC and FRAP, a quarter were intermediates on a FW basis, while there were more on a DW in contrast to TP. Therefore, there was a strong skew in TP toward low-parent types with a large percentage of low transgressive segregants, there being twice as many on a DW than FW basis. For TAC, there was no skew toward low-parent types, but there was skew toward low transgressive segregants that was slightly more pronounced on a DW than FW basis. For FRAP, there was a slight skew toward low-parent types and some skew toward low transgressive segregants, but the skew was more pronounced on a FW than DW basis, contrasting with TP and TAC. Overall, the Japanese/Kuril group showed a low to moderate proportion of additive gene action for TP, TAC and FRAP, with a substantial degree of transgressive segregation for the latter. Also, there was skew toward overdominance of low TP, TAC and FRAP as well as dominance of lower TP and FRAP contributed from the Kuril foundation group.

6.2.4.4 Improved Japanese/Russian Germplasm

For the Japanese/Russian group, TP ranged from 398.1-735.3 mg GAE/100 g FW and 2,643.6-5,778.9 mg GAE/100 g DW (**Figure 6.5**; **Table 6.11**). TAC ranged from 1.10-2.89 mmol TE/100 g FW and 7.33-24.33 mmol TE/100 g DW. FRAP ranged from 3.76-10.67 mmol AAE/100 g FW and 25.67-70.86 mmol AAE/100 g DW. The distribution of observations was predominantly unimodal for TP, in contrast to the bimodal distributions for the Japanese/Kuril and three foundation groups. For TAC, the distribution was more similar to the higher Russian group than the lower Japanese group, but the opposite was observed for FRAP. Comparison between the Japanese/Russian group and its parent groups was similar on a FW and DW basis for TP and both measures of AOA, the improved group overlapping the parent groups on the high ends but not the low.

For TP, there were more high than low transgressive segregants and parent types, while the majority were intermediates (**Figure 6.6**; **Appendix D.11**). For TAC, there was a much greater proportion of low transgressive segregants than high, but there were more high- than low-parent types, especially on a DW basis, leaving approximately a third as intermediates. For FRAP, there was a considerable number of low transgressive segregants and no high transgressive segregants, while skew toward low-parent types only manifested on a FW basis and intermediates comprised

a third on both a FW and DW basis. Therefore, there was heavy skew in TP toward high transgressive segregants and high-parent types but with a large proportion of intermediates. TAC showed skew toward low transgressive segregants and, contrastingly, high-parent types. FRAP manifested skew toward both low transgressive segregants and low-parent types, the latter being slight on a FW basis and heavy on a DW basis. For all three measures, skew was more pronounced on a DW than FW basis. In summary, there was a high proportion of additive gene action for TP and moderate proportion for TAC and FRAP with a low degree of transgressive segregation across all three traits. Nonetheless, there was clear skew toward dominance and overdominance of high TP, while there was overdominance of low TAC and FRAP but contrasting dominance of high Russian TAC on both a FW and DW basis and low Japanese FRAP on a FW basis only.

6.2.4.5 Improved Kuril/Russian Germplasm

For the Kuril/Russian group, TP ranged from 400.9-737.0 mg GAE/100 g FW and 2,732.7-5,629.6 mg GAE/100 g DW (**Figure 6.5**; **Table 6.11**). TAC ranged from 1.70-3.00 mmol TE/100 g FW and 9.34-24.37 mmol TE/100 g DW. FRAP ranged from 4.69-9.70 mmol AAE/100 g FW and 30.65-70.43 mmol AAE/100 g DW. The distribution of observations for TP was skewed toward the higher Russian group, and the distributions for TAC and FRAP were intermediate between the two parent groups. The Kuril/Russian group overlapped both extremes of its parent groups on a FW basis but did not overlap the lower end of the Russian group on a DW basis, whereas the improved group overlapped both ends of its parent groups on both a FW and DW basis for TAC and FRAP.

For TP, there was a preponderance of high transgressive segregants, no low transgressive segregants, some high-parent types, few low-parent types and many intermediates (**Figure 6.6**; **Appendix D.11**). For TAC and FRAP, there were similar proportions of low and high transgressive segregants while there were more low- and high-parent types on a FW basis only. A majority were intermediates for TAC on both a FW and DW basis, but less than a quarter and almost half were intermediates for FRAP on a FW and DW basis, respectively. Therefore, there was skew in TP toward high-parent types and, to a much greater extent, high transgressive segregants, especially on a FW basis. However, though TAC and FRAP were not clearly skewed in either direction on a DW basis, both measures of AOA had more low- than high-parent types on a FW basis only. Overall, the Kuril/Russian group showed a moderate to high proportion of

261

additive gene action for TP and FRAP and a very high proportion of additive gene action for TAC with an extensive degree of transgressive segregation for TP and low degree for TAC and FRAP. There was clear dominance and overdominance of high Russian TP, little skew in TAC and only some dominance of low Kuril FRAP on a FW basis, as for the Japanese/Russian group.

6.2.4.6 Mode of Gene Action across Improved Germplasm Groups

Across the improved germplasm, the total proportions of intermediates were high for TP and TAC on both a FW and DW basis. However, it was more moderate for FRAP, especially on a FW basis (**Figure 6.6**; **Appendix D.11**). Intermediates were most prevalent in the Japanese/Russian group for TP on a FW and DW basis and FRAP on a FW basis, while it was most prevalent in the Kuril/Russian group for TAC on a FW and DW basis and FRAP on a DW basis. For TP, intermediates predominated more on a FW than DW basis for the Japanese/Kuril group, while the opposite was seen for the other two groups. For TAC and FRAP, the Japanese/Kuril and Kuril/Russian groups had greater proportions of additive gene action on a DW than FW basis, and there was little difference in the Japanese/Russian group.

For TP, total transgressive segregation was higher in the Japanese/Kuril and Kuril/Russian groups than the Japanese/Russian group on a FW basis; Similarly, it was higher in the Japanese/Kuril than the Kuril/Russian group, which was higher than in the Japanese/Russian group on a DW basis. The opposite trend was seen for FRAP on a DW basis. Further, for TAC on both a FW and DW basis and for FRAP on a FW basis, there were no substantial differences in total transgressive segregation between improved groups. Averaged across improved groups, transgressive segregation was low in general but higher for TP than for TAC and FRAP, being higher on a FW than DW basis for TP but not contrasting for either TAC or FRAP.

Across groups, there was a slightly greater prevalence of high- than low-parent types but much greater prevalence of high compared to low transgressive segregants for TP, whereas low transgressive segregants were more pervasive than high for both TAC and FRAP. Further, TAC on a DW basis showed more high- than low-parent types, contrasting with FRAP on a FW basis, which presented far more low- than high-parent types. For TP, there was a skew toward the low transgressive segregants and low-parent types in the Japanese/Kuril group and a skew toward high transgressive segregants and high-parent types in the Japanese/Russian group and, to a greater degree, the Kuril/Russian group. For TAC, there was some skew toward low transgressive

262

segregants in the Japanese/Kuril and Japanese/Russian groups, a contrasting skew toward high-parent types in the Japanese/Russian group and a predominance of intermediates without substantial skew in the Kuril/Russian group. For FRAP, there was skew toward low transgressive segregants and low-parent types in the Japanese/Kuril and Japanese/Russian groups, being less pronounced for the latter group on a DW basis. Similarly, there was no skew on a DW basis for the Kuril/Russian group, but there was considerable skew toward low-parent types on a FW basis. In sum, the Japanese/Kuril group was skewed toward low-parent types for TP and FRAP and toward low transgressive segregants for all three traits. The Japanese/Russian and Kuril/Russian groups were skewed in the opposite direction to the Japanese/Kuril group for TP, toward high-parent types and high transgressive segregants, but had mixed trends in skew for TAC and FRAP. Specifically, their skew toward low transgressive segregants and high-parent types for TAC contrasted with the Japanese/Kuril group, while their skew toward both low transgressive segregants and low-parent types for FRAP mirrored the Japanese/Kuril group. The Kuril/Russian group had little skew for TAC and only skew toward low-parent types on a FW basis for FRAP, as for the Japanese/Kuril group.

The foundation groups did not contrast significantly for TP, so each improved group was an assortive cross. Nonetheless, the Japanese/Kuril group was skewed toward low transgressive segregants and low-parent types with a broader range and intermediate average to its parent groups. However, the other groups were skewed toward high transgressive segregants with narrow ranges and high averages. For TAC and FRAP, the Russian group was higher on average than the Kuril group, which was higher than the Japanese group. Comparison of parent genotypes for each family showed the Japanese/Kuril and Japanese/Russian groups were dissortive compared to the Kuril/Russian group. The Japanese/Kuril group showed skew toward lower Japanese FRAP but not TAC, manifesting skew toward low transgressive segregation for both TAC and FRAP. The Japanese/Russian group demonstrated skew toward higher Russian TAC on a FW and DW basis and lower Japanese FRAP on a FW basis only, but it showed low transgressive segregation for TAC and FRAP, as seen in the Japanese/Kuril group. The Kuril/Russian group showed skew toward lower Kuril FRAP on a FW basis only, as for the Japanese/Russian group, and no skew in transgressive segregation at all. Therefore, TP and measures of AOA combined in different ways depending on the foundation groups used to make each improved group.

6.2.4.7 Blueberry, Raspberry and Strawberry Compared to Improved Germplasm

The absolute phenotypic range in blueberry TP on a FW basis (110.9 mg GAE/100 g FW) was broader and narrower than the Japanese and Kuril groups, respectively, but consistently narrower than any blue honeysuckle group on a DW basis (254.7 mg GAE/100 g DW) (**Figure 6.5**; **Table 6.11**). The raspberry and strawberry ranges were slightly narrower than that of the Japanese group on a FW basis (68.7 and 52.4 mg GAE/100 g FW, respectively) and substantially narrower than any blue honeysuckle group on a DW basis (565.1 and 267.9 mg GAE/100 g DW, respectively). The average blueberry TP (373.7/2,444.7 mg GAE/100 g FW/DW) was lower than for any blue honeysuckle group on a FW or DW basis, the upper extreme overlapping the lower extremes of the Kuril, Russian and three improved groups on a FW basis but only the Russian and Japanese/Kuril groups on a DW basis. The average raspberry TP (505.2/3,324.7 mg GAE/100 g FW/DW) was higher than that of the Kuril, Russian and Japanese/Kuril groups and lower than that of the Japanese, Japanese/Russian and Kuril/Russian groups on a FW basis though higher than only the Russian group on a DW basis. The average strawberry TP (308.6/2,992.6 mg GAE/100 g FW/DW) was lower than for any blue honeysuckle group on a FW or DW basis, the highest strawberry extreme falling short of the lowest blue honeysuckle genotype on a FW basis but overlapping the lower end of each blue honeysuckle group on a DW basis.

The absolute phenotypic range in blueberry TAC was narrower than for each improved blue honeysuckle group. Compared to the Japanese group, this range was narrower (1.07 mmol TE/100 g FW) and broader (5.67 mmol TE/100 g DW) on a FW and DW basis, respectively. The raspberry range was also narrower than for any improved blue honeysuckle group, being slightly narrower (0.54 mmol TE/100 g FW) and broader (3.19 mmol TE/100 g DW) than the Russian group on a FW and DW basis, respectively. The range in strawberry TAC was close to that of the Kuril group on a FW basis (0.37 mmol TE/100 g FW) and the Russian group on a DW basis (2.83 mmol TE/100 g DW). The average blueberry TAC (1.23/7.97 mmol TE/100 g FW/DW) was substantially lower than for any blue honeysuckle group, but the highest extreme overlapped the lower ends of the Japanese and three improved groups. The raspberry average (2.39/15.68 mmol TE/100 g FW/DW) was close to the Kuril, Russian and Kuril/Russian groups, while it was higher than for the Japanese, Japanese/Kuril and Japanese/Russian groups. The average strawberry TAC (1.13/10.99 mmol TE/100 g FW/DW) was lower than the average for any blue honeysuckle group. Though the highest strawberry extreme did not overlap with any blue honeysuckle group on a DW

basis, the Japanese/Russian group overlapped the upper extreme and the Japanese/Kuril group overlapped both extremes on a FW basis.

The absolute phenotypic range in blueberry FRAP (2.17/8.66 mmol AAE/100 g FW/DW) was narrower than for any improved blue honeysuckle group though larger than for the Japanese and Kuril groups on a FW basis. The raspberry range (0.94/7.98 mmol AAE/100 g FW/DW) was far narrower than for any blue honeysuckle group on a FW basis, but slightly greater than for the Kuril group on a DW basis. The strawberry range (0.50/2.41 mmol AAE/100 g FW/DW) was far greater than for any blue honeysuckle group. The average blueberry FRAP (4.28/27.88 mmol AAE/100 g FW/DW) was lower than for any blue honeysuckle group. The lowest extreme was only slightly less than those of the Japanese/Russian and Kuril/Russian groups and greater than that of the Japanese/Kuril group. However, the high extreme was well within the range of each improved group. The raspberry average (4.46/29.41 mmol AAE/100 g FW/DW) was lower than the averages for any improved group, but the low extreme was close to that of each improved group, and the high extreme was well within the range of each improved group. The strawberry average (2.43/23.56 mmol AAE/100 g FW/DW) was considerably lower than any blue honeysuckle group average, and the high extreme was lower than any blue honeysuckle genotype on a FW basis and all but the lowest extreme in the Japanese/Kuril group on a DW basis.

6.2.4.8 Correlations between Traits Contributing Potential Human Health Benefits

Positive correlations between FW and DW measures of TP, TAC and FRAP were moderate to high across the foundation and improved blue honeysuckle germplasm combined (**Table 6.13**). In each foundation group on its own, these correlations were high to very high, while they were moderate to high for the Japanese/Kuril and Japanese/Russian groups on their own and high in the Kuril/Russian group on its own.

Across the foundation and improved blue honeysuckle germplasm, there were moderate positive correlations between TP and TAC and between TP and FRAP on a FW basis. Across the foundation germplasm on its own, the former correlation was high for each group and the latter was moderate, high and very high in the Japanese, Russian and Kuril groups, respectively. In the improved groups on their own, the correlation between TP and TAC was moderate in the Japanese/Kuril and Japanese/Russian groups and low in the Kuril/Russian group. The correlation between TP and FRAP was low for the Japanese/Kuril and Kuril/Russian groups and moderate for

Table 6.13. Foundation and Improved Germplasm: Pearson's correlations between biochemical determinations of nutritional content for blue honeysuckle in 2012/2013 in Chilliwack, BC, Canada (only statistically significant correlations [$p < 0.05$] are shown, FW – fresh weight, DW – dry weight, GAE – gallic acid equivalents, TE – Trolox equivalents, AAE – ascorbic acid equivalents).

		Group	r			Group	r
Total Phenolics (mg GAE/100 g FW)	Total Phenolics (mg gallic acid equivalents/100 g DW)	All Germplasm	0.757	Trolox Antioxidant Capacity (mmol TE/100 g FW) at 5 minutes	Trolox Antioxidant Capacity (mmol TE/100 g DW) at 5 minutes	All Germplasm	0.705
		Japanese	0.802			Japanese	0.901
		Kuril	0.933			Kuril	0.974
		Russian	0.841			Russian	0.856
		Japanese/Kuril	0.752			Japanese/Kuril	0.609
		Japanese/Russian	0.747			Japanese/Russian	0.717
		Kuril/Russian	0.774			Kuril/Russian	0.727
	Trolox Antioxidant Capacity (mmol TE/100 g FW) at 5 minutes	All Germplasm	0.560		Ferric Reducing Antioxidant Potential (mmol AAE/100 g FW) at 4 minutes	All Germplasm	0.787
		Japanese	0.703			Japanese	0.793
		Kuril	0.828			Kuril	0.851
		Russian	0.838			Russian	0.799
		Japanese/Kuril	0.626			Japanese/Kuril	0.701
		Japanese/Russian	0.541			Japanese/Russian	0.841
		Kuril/Russian	0.480			Kuril/Russian	0.760
	Ferric Reducing Antioxidant Potential (mmol AAE/100 g FW) at 4 minutes	All Germplasm	0.535	Ferric Reducing Antioxidant Potential (mmol AAE/100 g FW) at 4 minutes	Ferric Reducing Antioxidant Potential (mmol AAE/100 g DW) at 4 minutes	All Germplasm	0.699
		Japanese	0.569			Japanese	0.924
		Kuril	0.908			Kuril	0.965
		Russian	0.859			Russian	0.937
		Japanese/Kuril	0.417			Japanese/Kuril	0.569
		Japanese/Russian	0.524			Japanese/Russian	0.674
		Kuril/Russian	0.491			Kuril/Russian	0.730

the Japanese/Russian group. Further, there were high positive correlations between TAC and FRAP across the foundation and improved germplasm and within foundation and improved groups on a FW basis.

In addition to these phenotypic correlations in blue honeysuckle, hybrid/parent comparisons (i.e., correlations between statistical classifications of hybrid genotypes) were correlated across the improved germplasm. These correlations were moderate for TP with TAC and for TAC with FRAP but low for TP with FRAP (**Table 6.14**). In the Japanese/Kuril group on its own, these correlations were moderate for TP with TAC and FRAP and high for TAC with FRAP. In the Japanese/Russian group, they were low and moderate for TP with TAC and FRAP, respectively, and high for TAC with FRAP. These correlations were universally low in the Kuril/Russian group.

Table 6.14. Improved Germplasm: Rho correlations between statistical classifications of hybrid blue honeysuckle genotypes for nutritional content traits in 2012/2013 in Chilliwack, BC, Canada (only statistically significant correlations [$p < 0.05$] are shown, FW – fresh weight, DW – dry weight, GAE – gallic acid equivalents, TAC – Trolox Antioxidant Capacity, TE – Trolox equivalents, FRAP – ferric reducing antioxidant potential, AAE – ascorbic acid equivalents).

		Group	r			Group	r
Total Phenolics (mg GAE/100 g FW)	TAC (mmol TE/100 g FW) at 5 min	All Improved	0.501	Total Phenolics (mg GAE/100 g DW)	FRAP (mmol AAE/100 g FW) at 4 min	All Improved	0.374
		Japanese/Kuril	0.636			Japanese/Kuril	0.593
		Japanese/Russian	0.640			Japanese/Russian	0.417
		Kuril/Russian	0.331			Kuril/Russian	0.355
	TAC (mmol TE/100 g DW) at 5 min	All Improved	0.372		FRAP (mmol AAE/100 g DW) at 4 min	All Improved	0.454
		Japanese/Kuril	0.713			Japanese/Kuril	0.819
		Japanese/Russian	0.411			Japanese/Russian	0.485
	FRAP (mmol AAE/100 g FW) at 4 min	All Improved	0.490	TAC (mmol TE/100 g FW) at 5 min	FRAP (mmol AAE/100 g FW) at 4 min	All Improved	0.662
		Japanese/Kuril	0.678			Japanese/Kuril	0.785
		Japanese/Russian	0.450			Japanese/Russian	0.784
		Kuril/Russian	0.440			Kuril/Russian	0.529
	FRAP (mmol AAE/100 g DW) at 4 min	All Improved	0.389		FRAP (mmol AAE/100 g DW) at 4 min	All Improved	0.541
		Japanese/Kuril	0.681			Japanese/Kuril	0.710
		Japanese/Russian	0.425			Japanese/Russian	0.659
Total Phenolics (mg GAE/100 g DW)	TAC (mmol TE/100 g FW) at 5 min	All Improved	0.323			Kuril/Russian	0.323
		Japanese/Kuril	0.555	TAC (mmol TE/100 g DW) at 5 min	FRAP (mmol AAE/100 g FW) at 4 min	All Improved	0.491
		Japanese/Russian	0.401			Japanese/Kuril	0.729
	TAC (mmol TE/100 g DW) at 5 min	All Improved	0.485			Japanese/Russian	0.623
		Japanese/Kuril	0.847			Kuril/Russian	0.317
		Japanese/Russian	0.517		FRAP (mmol AAE/100 g DW) at 4 min	All Improved	0.664
						Japanese/Kuril	0.945
						Japanese/Russian	0.768
						Kuril/Russian	0.421

7. CHAPTER 7: GENERAL DISCUSSION AND CONCLUSIONS

7.1 Inferences

As a novel crop, blue honeysuckle stands out for its high antioxidant content (Chaovanalikit et al 2004), early-season fruiting (Plekhanova 1994a), extreme winter hardiness (Imanishi et al 2000), unique flavor and aroma profiles (Thompson and Barney 2007) and diverse fruit shapes (Bors et al 2012). Though genetic progress is ongoing (Bors et al 2015), breeding is in early stages compared with most large-scale commercial fruit crops. Blue honeysuckle domestication occurred recently, and breeding efforts have predominantly relied on selection from open-pollinated (OP) seed (Kuklina 2009). Therefore, current cultivars are generally two or three generations removed from the wild and have limitations to large-scale production (Plekhanova 1994a; Zholobova and Khokhyrakova 2009). Though naturally adapted to cold climates, breeding for temperate climates that are suited to large-scale horticultural production has received little attention (Thompson 2006b). There are three primary barriers: 1) low chilling requirement, resulting in early bud break, winter damage and poor pollination in temperate climates (Sarja 1998); 2) modest yields, irregular fruit shapes and agronomic traits that limit harvestability and marketability (Suzuki et al 2007); and 3) low TSS:TA (Thompson 2006b) with questionable claims of potential human health benefits due to widely varying claims of AOA (Thompson and Chaovanalikit 2003; Rupasinghe et al 2012). Characterizing genetic resources and modes of gene action for phenological, morphological and biochemical traits is essential to developing breeding strategies that overcome barriers to large-scale commercial production in temperate climates.

The hypothesis of the current thesis was that blue honeysuckle germplasm contains phenological, morphological and biochemical variability that will facilitate development of a commercial crop suited to large-scale production in temperate climates. Using foundation germplasm groups from Japan, the Kuril Islands and Russia, as well as improved hybrid groups between them, diversity in these features was evaluated in the Fraser Valley, a major temperate climate fruit production region. Three large-scale commercial crops, highbush blueberry, red raspberry and June-bearing strawberry, provided direct, biologically-replicated comparisons. The current work characterizes genetic variability in foundation groups, demonstrates the diverse ways in which this variation combines in improved groups and elucidates the genetic and physiological complexity of these traits. Specifically, there is phenological variation permitting adaptation to a temperate climate, fruit morphological diversity indicating large-scale commercial agronomic

potential and fruit biochemical traits signifying commercially marketable FQ in addition to high nutritional content related to potential human health benefits. The following is a summary of the supporting evidence.

7.2 Phenology

7.2.1 Spring Phenology

7.2.1.1 Foundation Germplasm

With some overlap, foundation group membership was the principal feature of diversity in temperate climate phenological adaptation. Extremely early phenology, primarily in the Russian group, relates to adaptation to cold climates at high latitudes with short growing seasons. This indirectly limits production in a temperate climate by permitting active growth during winter months and onset of bloom during poor pollination conditions, confirming observations in Russia (Plekhanova 1994a) and Corvallis (Thompson and Barney 2007). The Japanese group bloomed earlier than blueberry, raspberry and strawberry but still set fruit well due to its adaptation to lower latitudes, longer growing seasons and less severe winter conditions. The relatively homogenous Kuril group broke bud at the same time (but bloomed earlier) than blueberry and raspberry while overlapping in fruit harvest with strawberry. Therefore, the blue honeysuckle foundation germplasm has a broad range of genetic variability for suitable phenological adaptation to a temperate climate. Crossing the Russian germplasm with the Japanese and Kuril germplasm requires selection against early phenology, while selecting for later flowering onset is important when using all three foundation groups.

Compared to cold climates, blue honeysuckle broke bud much earlier in the Fraser Valley's high chill environment, but this distinction narrowed through bloom. This distinction was also minimal for the Russian group and non-existent for the Japanese group at fruit harvest. Phenological progression varied across groups, and differences between groups diminished over the course of spring development. Therefore, variation in the underlying physiological responses to environmental conditions present an opportunity to make genetic progress. Differential progression through spring phenophases and across foundation groups compared to cold climates implies the potential to simultaneously enhance the earliness in fruit harvest while improving adaptation by selecting for later bud break and bloom (**Figure 7.1**).

Intermediate Japanese phenology → Dominance and overdominance → Late Kuril phenology

Japanese/Kurils:

- Dominance and overdominance of earlier phenology – maintain early-season advantage
- Additivity for flowering onset – maintain pollination and extend season

Dominance and overdominance

Additivity

Japanese/Russian:

- Dominance and overdominance of later phenology – introgression of Russian fruit traits
- Fruit ripening during warmer conditions – increase fruit quality
- Dominance of later growth cessation and both dominance and overdominance of later leaf drop – improve adaptation

Kuril/Russian:

- Additivity – can select against poor Russian adaptation for all phenophases

Early Russian phenology

Figure 7.1. Foundation and Improved Germplasm: Key opportunities for enhancing temperate climate adaptation in blue honeysuckle.

271

7.2.1.2 Improved Germplasm

There was dominance and overdominance of intermediate Japanese over late Kuril phenology, being more evident at bud break than at bloom or harvest (**Figure 7.1**). Similarly, intermediate Japanese phenology varied in its dominance and overdominance over early Russian phenology across spring phenophases. The late Kuril and early Russian groups combined additively with a slight skew toward dominance of early Russian phenology at bud break. Therefore, the improved groups compared with their respective parent groups in different ways, suggesting genetic complexity in phenological adaptation. Intermediate Japanese phenology moderates the early Russian and late Kuril phenologies through both dominant and overdominant gene action, while the extremes combine additively to make intermediate phenology.

Phenology in the Japanese/Kuril group ranged later, coming closer to that of the three comparison crops, but the Japanese/Russian group showed potential to select for later bud break and bloom while accessing Russian genetics due to a tendency to produce late transgressive segregants. Prevalent early transgressive segregation for harvest date and high proportions of additive gene action for flowering onset in the Japanese/Kuril group should make it possible to select for earlier harvest while maintaining a suitable bloom period during good pollination conditions. Further, the Japanese/Kuril and Japanese/Russian groups had late transgressive segregants, permitting season extension to overlap more with the timing of large-scale commercial crops when higher ambient temperatures may lead to better FQ. Generally, high H^2 will facilitate phenological selection for enhanced temperate climate adaptation but to different extents across groups and phenophases. Long-term genetic gains can be achieved for the most important trait relating to productivity (i.e., flowering onset), which can be utilized most effectively using Japanese/Kuril blue honeysuckle populations to enhance adaptation to temperate climates.

7.2.2 Vegetative Growth Cessation and Leaf Drop
7.2.2.1 Foundation Germplasm

Further, while spring phenological development was closely related to accumulation of growing degree units after release from dormancy, vegetative growth cessation and leaf drop showed the importance of day-length cues, related to latitude of provenance, with modulation by other environmental factors. Consequently, very rapid floral initiation in blue honeysuckle is related to adaptation to short growing seasons at higher latitudes. This presents a direct barrier to

crop adaptation to more southern latitudes due to secondary flowering, late flushes of growth and early summer dormancy that detract from productivity in the following year (**Figure 7.1**).

7.2.2.2 Improved Germplasm

For growth cessation and leaf drop, there was lower H^2 and h^2 than observed for the spring phenophases, which will make selection and genetic progress more difficult, respectively (**Figure 7.1**). The improved groups had broad but similar ranges for these phenophases due to different modes of gene action between foundation groups. The Japanese/Kuril group displayed overdominance and some dominance of early growth cessation but, contrastingly, of late leaf drop. The Japanese/Russian group showed dominance of late growth cessation and both dominance and overdominance of late leaf drop with primarily additive gene action. The Kuril/Russian group did not manifest any transgressive segregation or skew in dominance but combined additively for growth cessation. Likewise, it showed some skew toward later leaf drop but primarily additive gene action. Compared to blueberry and raspberry, early growth cessation and leaf drop are not direct limitations to blue honeysuckle growth and development, but they are related to poor adaptation to fluctuating winter temperatures. Fortunately, skew toward later leaf drop will produce a high proportion of improved genotypes with better temperate climate adaptation, especially in the Japanese/Kuril group.

7.3 Morphology
7.3.1 Quantitative Measures of Agronomic Potential
7.3.1.1 Foundation Germplasm

Russian fruit weight, length and width were within ranges observed in a variety of cold Eurasian climates (Kolasin and Pozdynakov 1991; Petrushua 2009) and in Saskatchewan (Bors et al 2009). Though peak yields were not assessed, greater overall yield potential in the Fraser Valley is implied since Japanese genotypes in the current trials had equivalent yields in early years of production to some of the maximum yields observed in Japan (Nakajima 1996). In contrast, Russian germplasm is unlikely to reach yields observed in cold climates (Plekhanova 1998) due to poor phenological adaptation.

As a niche-market crop with limited exposure to intensive production practices in major fruit production regions, it should not be assumed that commercial blue honeysuckle cultivation

requires limited fertility, irrigation, pest and disease management or that this is an advantage over other crops. To the contrary, development of pest and disease issues that necessitate direct management is inevitable. Use of fertilizer, irrigation and integrated pest and disease management to leverage advancing blue honeysuckle genetics to attain their optimal fruit yield and quality is important for the transition from a niche to a large-scale commercial crop. Corresponding intensive monoculture practices will likely be necessary to emulate successes in other crops, which compete for land, labour and marketability in regions with temperate climates and well-established fruit industries. Additionally, as for any other crop, large-scale production demands development of cultivar-specific management practices that optimize fruit yield and quality.

Within the Japanese group, greater fruit weight was more directly related to fruit length than width, whereas higher yields and greater fruit weight were not closely related (**Figure 7.2**). The Kuril group had low variability in agronomic potential but exhibited a relationship between higher width to weight ratios (i.e., greater density) and greater fruit weight, length and width. Various combinations of fruit length, width and density produced a range in Russian fruit weights, linking low agronomic potential in this group to poor phenological adaptation and fruit set.

7.3.1.1 Improved Germplasm

Across the blue honeysuckle germplasm, fruit width had greater H^2 than weight and length, yield having considerably lower H^2 (**Figure 7.2**). The Japanese group had the highest H^2 for yield, weight and length, and the Kuril group had the highest H^2 for width. Moreover, negligible H^2 was found for yield in the Kuril group and for width in the Russian group, the latter showing low H^2 for the other traits. In the improved germplasm, H^2 was higher for fruit weight than length, which was higher than for width. Yield had universally low H^2, but the Japanese/Kuril group had the highest H^2 for weight, length and width, followed by the Japanese/Russian group and then the Kuril/Russian group. In contrast, for fruit yield and weight, h^2 was higher for yield and weight than for length and width across the improved germplasm. Specifically, h^2 for the Japanese/Kuril group was greatest for weight followed by width, length and yield in descending order. For the Japanese/Russian group, h^2 was greater for weight than length, whereas, for the Kuril/Russian group, h^2 was only considerable for length.

Though additive gene action ranged from moderate to high for yield, there was no over-arching trend in overdominance, and dominance was only seen for higher Japanese yields in the

Japanese

- High yields – not closely related to weight
- Large fruit size – related to fruit length
- Highest H^2 for yield, weight, length

Japanese/Russian

- Intermediate H^2 for weight, length and width
- h^2 for weight > length
- Dominance of higher Japanese yield

Overall

- Additivity moderate to high for yield; low to moderate for length; and low for weight and width
- H^2 for width > weight ≈ length > yield
- h^2 for yield ≈ weight > length ≈ width
- Dominance and overdominance of heavy, wide fruit no matter the source

Japanese/Kurils:

- Highest H^2 for weight, length and width
- h^2 for weight > width > length > yield
- Dominance of shorter Kuril fruit

Kuril

- Intermediate yields
- Highest H^2 for width

Kuril/Russian

- Low H^2 for weight, length and width
- h^2 only considerable for length
- Dominance of long Russian fruit

Russian

- Low yield – related to poor adaptation rather than length, width or weight

Figure 7.2. Foundation and Improved Germplasm: Key opportunities for enhancing morphological features related to agronomic potential in blue honeysuckle.

assortive Japanese/Russian group. While additive gene action ranged from low to moderate for length, there was dominance of shorter Kuril fruit in the dissortive Japanese/Kuril group contrasting with dominance of longer Russian fruit in the dissortive Kuril/Russian group. However, there was a lack of skew in the assortive Japanese/Russian group. For weight and width, additive gene action was low and transgressive segregation was high for the assortive Japanese/Kuril and Kuril/Russian groups, but the opposite was observed for the dissortive Japanese/Russian group. Invariably, there was skew toward dominance and overdominance of heavy, wide fruit, no matter the genetic source.

7.3.2   Fruit Shapes Associated with Agronomic Potential

7.3.2.1 Foundation Germplasm

Fruit shapes are not only highly variable between blue honeysuckle genotypes, but vary dramatically within genotypes and even within harvests from individual plants, manifesting one to four distinguishable fruit shapes at the same time, depending on environmental factors that affect fruit development. Within-genotype diversity in fruit shape was low for the Russian group and high in the Kuril and Japanese groups, and between-genotype diversity was low in the Kuril group and high in the Japanese and Russian groups. Different manifestations of diversity in fruit shapes across foundation groups is related to blue honeysuckle's unique fruit anatomy as a multiple fruit formed by synanthy of accessory tissues. Specifically, the fruit of blue honeysuckle is a pseudocarp formed by false synanthy with a cupula comprised of four bractlets.

Blue honeysuckle is prone to developmental abnormalities, principally incomplete synanthy of the fruit capsule. While these environmentally-regulated phenomena have a genetic basis, more routine variation in shape is associated with the fact that the ovaries are completely free of one another inside the bracteolar sheath. Variability in the length of the capsule relative to the enclosed fruit, the position of the fruit within the capsule and the size and shape of the true fruit within results in a broad range of overall fruit shapes, proximal and distal end shapes and degrees to which the distal end opens and the accessory layer rolls back upon itself (**Figure 7.3**). The distal end of the fruit can be either separated from the outer accessory layer, or in close contact with it, but not actually physically fused. The variable appearance of the distal end is related to the degree of contact between the accessory layer and distal fruit tissues as well as the relative lengths of these tissues. Moreover, the shape and distribution of the fruit within the accessory

Width

Fruit-pedicel
junction (bracts
included for
orientation)

Twin simple fruit

Location of false
fruit synanthy

Accessory layer of
bract tissue

Fruit calices

Termination of
accessory layer

Proximity of
calices to
accessory
margin

Length of Accessory Layer

Length of Fruit

Anatomy of fruit shape variation:

- Length of accessory capsule relative to enclosed fruit
- Size and shape of fruit within
- Position of fruit within capsule
- Proximal and distal end shapes
- Size of opening and/or rolling of distal end of accessory tissue
- Calices separated or contacting margin of accessory tissue

Sources of Variation:

Group	Within-genotype	Between-genotype
Japanese	High	High
Kuril	High	Low
Russian	Low	High

Figure 7.3. Foundation and Improved Germplasm: Anatomical basis for variation in fruit shape in blue honeysuckle.

layer complicates fruit shape morphology, interacting with various combinations of proximal and distal end shapes to result in associations between distinct fruit shapes. Genetic factors, in turn, interact with environmental factors (e.g., weather, temperature, moisture, nutrition and crop load) that influence pollination, fruit set and fruit development.

7.3.2.2 Improved Germplasm

Ovate and oblong shapes were detected across all foundation and improved groups. Cylindrical shapes were discovered in the Japanese and Kuril groups but not the Russian group or any improved group. Bottle shapes were found in the Japanese and Russian groups but not the Kuril group or any improved group. Correspondingly, spindle shapes were found in the Japanese and Russian groups but not the Kuril group, being rare in the Japanese/Russian and Kuril/Russian groups and absent from the Japanese/Kuril group. Torpedo shapes were found in only the Japanese foundation group but were seen in all three improved groups. Bell and pear shapes were only found in the Russian foundation group but were observed in all three improved groups.

Oblong shapes, which were the most prevalent $1°$ and $2°$ shapes in both the foundation and improved germplasm, are rounded at both ends, and the fruit within have a consistent width. Cylindrical shapes found in the Japanese and Kuril groups are a blockier variant of oblong shapes, likely relating to greater proportional development of the accessory layer at both ends relative to the fruit within, which makes the proximal end shapes truncate and distal end shapes flat or even indented. Ovate shapes are intermediate between cylindrical and oblong shapes with more similarity to the former at the proximal end and to the latter at the distal end, which results in tapering. Torpedo shapes were associated with the basic ovate, oblong and cylindrical shapes as well as bottle shapes. Bottle shapes were associated with oblong and cylindrical as well as ovate shapes. Bell and pear shapes were associated with oblong, cylindrical and bottle shapes. Spindle shapes were associated with oblong, ovate and bottle shapes in the foundation germplasm and with pear and bottle shapes in the improved germplasm.

These associations suggest that a peaked distal end will result in a torpedo shape overall if the factors that lead to a more tapered distal end are accompanied by greater elongation of the outer accessory layer in conjunction with relatively short fruit within (**Figure 7.4**). While the development of the accessory tissue is greater than the fruit within for the distal end of the ovate and torpedo shapes, this is exaggerated in bottle shapes, resulting in a distinct

278
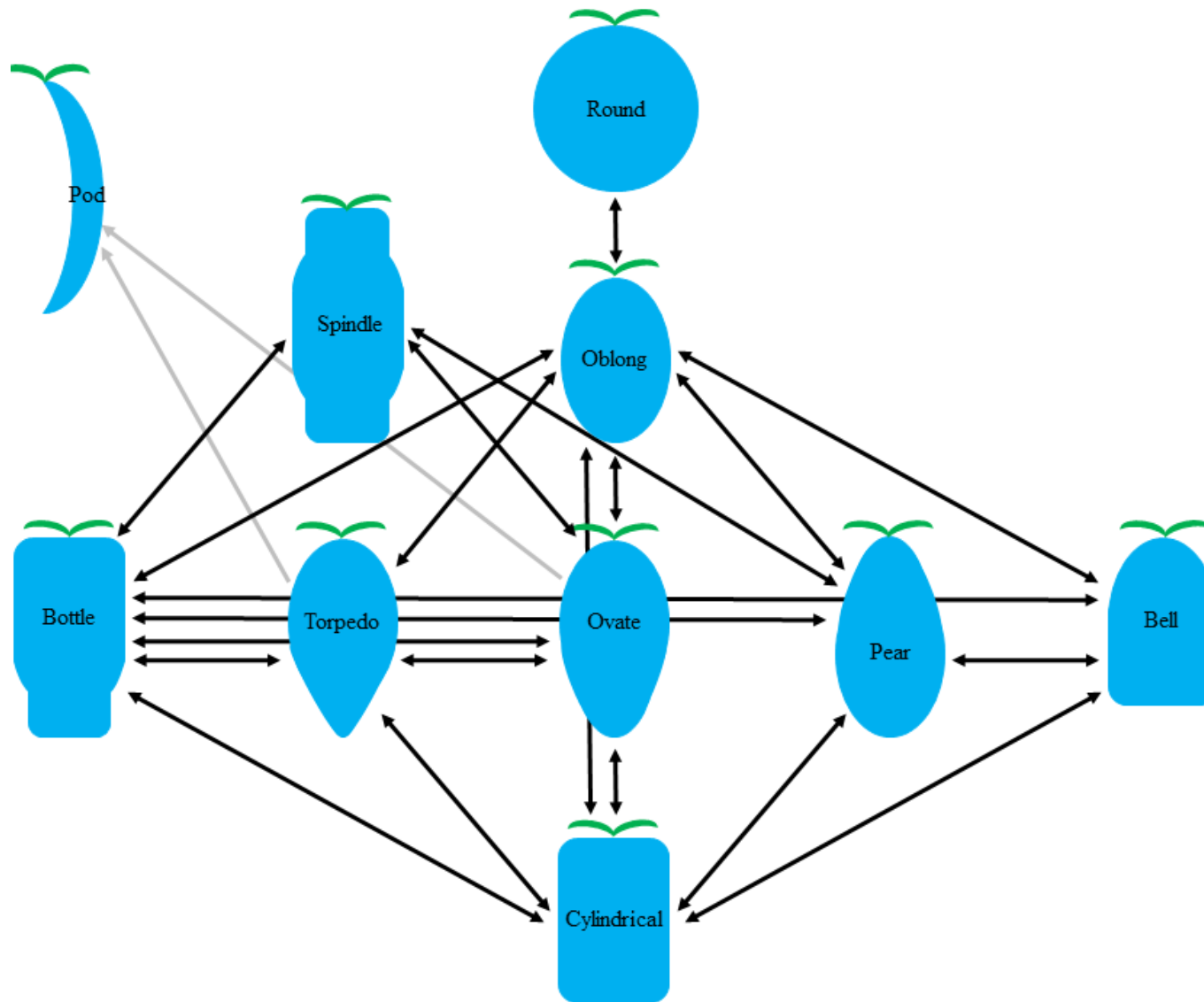
Figure 7.4. Foundation and Improved Germplasm: Fruit shape associations in blue honeysuckle germplasm evaluated in 2012/2013 in the Fraser Valley, BC, Canada in 2012/2013 (Grey – developmental abnormality, Black – shape associations).

constriction of the distal region. Bell shapes are characterized by an over-developed accessory layer at the proximal end more than a relative imbalance in the distribution of fruit toward the distal end. Pear shapes are characterized by a relative imbalance in the distribution of fruit toward the distal end more than over-development of the accessory layer toward the proximal end. Therefore, bell shapes can be considered an open-ended form of pear shapes. Spindle shapes have an imbalanced distribution of fruit tissues, resulting in a constricted region at the proximal end, as well as an over-development of the distal end of the accessory layer, making a constricted distal region as for bottle shapes.

7.3.3   Qualitative Measures of Agronomic Potential

7.3.3.1 Foundation Germplasm

The Japanese and Russian groups demonstrated variability for completeness of synanthy, evenness of fruit surface, fruit colour, distal end opening size and fruit taste (**Table 7.1**). While the Japanese group was also an important source of variation in fruit aroma, the Russian group contained variation in fruit firmness, strength of attachment and picking scar quality. The Kuril group had relatively low variation for most traits. However, the Kuril group was the most consistent source of complete synanthy, even fruit surface, small distal opening size, low heterogeneity in fruit shape and size as well as sweet fruit taste. The Japanese and Russian groups stood out for lack of fruit pubescence, heavy fruit bloom and broad shape in cross-section. The Russian group was singular for its strong fruit aroma, while the Japanese group contributed the firmest fruit, loosest attachment, lowest degree of harvest contamination with stems and consistently small, dry picking scars. Prevalence of fruit mold was generally low across foundation groups but demonstrated a correlation with later phenology, being worse in the Kuril group than the Japanese group for which it was worse than the Russian group.

A relative selection index (SI) provides corroboration of these findings, demonstrating which traits have important negative and positive effects on overall agronomic potential from each group. In general, the Japanese group had a moderate phenotypic range for overall agronomic potential because it had average ratings for most traits. The Kuril group showed a very narrow phenotypic range in overall agronomic potential, but most traits were either highly positive or highly negative. The Russian group had the broadest phenotypic range in agronomic potential, with a greater number of important positive traits than negative.

Table 7.1. Foundation and Improved Germplasm: Variation and heritability for fruit morphological ratings related to agronomic potential in blue honeysuckle evaluated in 2012/2013 in the Fraser Valley, BC, Canada.

	Source of Variation			Best Genetic Source			High H^2			High h^2			
	Japanese	Kuril	Russian	Japanese	Kuril	Russian	Japanese/ Kuril	Japanese/ Russian	Kuril/ Russian	All Improved	Japanese/ Kuril	Japanese/ Russian	Kuril/ Russian
Fruit Synanthy	✓	✓			✓		✓	✓	✓	✓	✓		
Fruit Surface	✓	✓			✓		✓	✓	✓	✓	✓	✓	
Fruit Pubescence				✓		✓	✓	✓	✓	✓	✓		✓
Fruit Bloom				✓		✓		✓	✓		✓		
Fruit Colour	✓	✓							✓	✓	✓		
Fruit Shape in Cross-Section				✓		✓	✓	✓		✓			
Distal Opening Size	✓	✓			✓		✓						
Heterogeneity of Fruit Size					✓								
Heterogeneity of Fruit Shape					✓								
Fruit Taste	✓	✓			✓		✓	✓	✓		✓		
Fruit Aroma	✓					✓	✓	✓	✓		✓	✓	
Fruit Mold						✓	✓	✓	✓				
Fruit Flesh Firmness		✓		✓			✓	✓	✓				
Strength of Attachment		✓		✓				✓					✓
Stems Retained in Harvest				✓			✓	✓		✓			✓
Picking Scar Quality		✓		✓				✓				✓	✓

7.3.3.2 Improved Germplasm

Total absence of incomplete synanthy was observed in genotypes in each improved group (**Table 7.1**). Therefore, efforts to select against this negative trait will be successful in combining all three foundation groups. Equally, with very even fruit surface ratings observed in each improved group, producing improved genotypes with fruit surface characteristics that facilitate ease of rolling during harvest and sorting is possible by crossing with even the highly uneven fruit in the Russian group. Similarly, selection against fruit pubescence contributed by the Kuril group will be facilitated by high H^2 across improved groups. Improvement upon weaker fruit bloom from the Japanese and Kuril groups will be facilitated by dominance and overdominance of heavier bloom from the Russian group. The Russian and Kuril groups combine best to consistently make darker colours. Variation in fruit shape in cross-section will make it possible to select against the more elliptical shapes contributed by the Russian and Kuril groups, but crosses with the more circular Japanese genetics are most likely to result in circular shapes in cross-section. The apparent dominance and overdominance of larger distal opening sizes contributed by the Russian group present an opportunity to create unique and interesting fruit shapes for the home garden. Conversely, this is a challenge to breeding cultivars with better commercial agronomic potential with uniform fruit appearance and lower susceptibility to damage during harvest and sorting. Therefore, crossing the Japanese and Kuril groups is the best strategy.

Heterogeneity in fruit size and shape had lower H^2 than other characteristics, which was likely due to the inadequacy of phenotyping by visually inspecting harvested fruit *en masse*. Therefore, selection for improved uniformity will require development of a better quantitative measure that can be applied at later selection stages, facilitating larger volumes of fruit. In contrast, selection of sweeter and more aromatic genotypes with lower incidence of mold and firmer flesh should be possible in any one generation due to high H^2, but no single combination of foundation groups can be recommended over the others. Strength of fruit attachment has high H^2, which presents an important opportunity to enhance one the key advantages of blue honeysuckle over crops such as blueberry, raspberry and strawberry: the ability to simultaneously harvest all fruit on a plant. Pre-harvest shattering is observed in other regions (Korobkova 2009; Murslimova 2013), but did not occur to any considerable extent in the Fraser Valley. Consequently, development of cultivars with loose attachment, especially using the Japanese and Russian groups, stands to make a significant improvement in the efficiency of blue honeysuckle cultivation for temperate climates.

Further, indications of dominant gene action for fewer stems in harvested fruit point toward crosses with the Japanese group to reduce harvest contamination. Consistently dry picking scars will likely be found most often in combinations of the Japanese and Russian group, whereas more intense negative selection will be required in the Kuril/Russian group. In contrast, wet picking scars were least prevalent in the Kuril/Russian group despite being more common in the Kuril and Russian groups than the Japanese group.

Long-term genetic progress for incidence of incomplete synanthy, fruit surface evenness, pubescence, colour, shape in cross-section and presence of stems in harvested fruit can be expected across the improved germplasm. Additive gains will be most easily achieved for fruit synanthy, bloom, colour and taste in the Japanese/Kuril group; fruit attachment and presence of stems in harvested fruit in the Japanese/Russian group; fruit surface, aroma and picking scar quality in the Japanese/Kuril and Japanese/Russian groups; and fruit pubescence in the Japanese/Kuril and Kuril/Russian. Fruit shape in cross-section did not demonstrate considerable additive gene action in any individual improved group as it did across the improved germplasm. Distal opening size, heterogeneity in size and shape, incidence of mold and flesh firmness did not have appreciable additive gene action in either improved groups on their own or across the improved germplasm, so long-term gains will also be difficult. Further, a relative SI shows variability in fruit traits related to agronomic potential between groups, which suggest the ability to select parental combinations to make genetic improvements for each morphological feature.

7.4 Biochemistry
7.4.1   Fruit Quality
7.4.1.1 Foundation Germplasm

DM was high in both the Japanese and Russian groups compared with the Kuril group, but the genotypes with the highest and lowest average values were both in the Russian group (**Table 7.2**). In contrast, the Japanese group had higher average TSS as well as the genotype with the highest value. The averages for the Kuril and Russian groups were lower, and the lowest genotype was in the latter group. For TA, the Kuril group was intermediate to the high Japanese and low Russian groups, which had the highest and lowest genotypes, respectively. The opposite trends were seen for pH. Similar to pH, the Japanese group had the lowest average TSS:TA and the Russian group the highest, but both the highest and lowest phenotypic extremes were found in the

283

Table 7.2. Foundation Germplasm: Group averages, and high and low phenotypic extremes, for biochemical determinations of fruit quality and nutritional content in blue honeysuckle germplasm evaluated in 2012/2013 in the Fraser Valley, BC, Canada (TAC – Trolox antioxidant capacity, FRAP – ferric reducing antioxidant potential).

	Japanese			Kuril			Russian		
	Average	Lowest	Highest	Average	Lowest	Highest	Average	Lowest	Highest
Dry matter	High			Low			High	✓	✓
Total soluble solids	High		✓	Low			Low	✓	
Titratable acidity	High		✓	Intermediate			Low	✓	
pH	Low	✓		Intermediate			High		✓
Total soluble solids:Titratable acidity	Low	✓	✓	Intermediate			High		
Total phenolics (fresh weight)	Low	✓		Intermediate			High		✓
Total phenolics (dry weight)	Low	✓		Intermediate			High		✓
TAC (fresh weight)	Low	✓		High			High		✓
TAC (dry weight)	Low	✓		High		✓	Intermediate		
FRAP (fresh weight)	Low	✓		High			High		✓
FRAP (dry weight)	Low	✓		High			High		✓

Japanese group. Compared to the literature, DM was higher in the Fraser Valley's temperate climate than in the coldest of continental climates where superior climatic adaptation permits full pollination to stimulate more complete fruit development. TSS was lower and TA was higher than reported from colder climates, which was due to different methods and environments across studies.

Direct field comparison with large-scale commercial crops demonstrated DM for blue honeysuckle was intermediate to the lower strawberry and the higher blueberry and raspberry ranges. Similarly, blueberry had a higher average TSS than raspberry, which had intermediate TSS to the higher Japanese and lower Kuril and Russian blue honeysuckle averages, which all had much higher averages than the strawberry. In contrast, all three comparison crops had lower average TA than any blue honeysuckle foundation group, and only the highest TA observed in raspberry overlapped the low extremes of each blue honeysuckle foundation group. Average pH for blueberry and raspberry was close to the averages for the blue honeysuckle foundation groups, while strawberry had a considerably higher average. Though TSS:TA was higher for blueberry and strawberry, the range in TSS:TA for all three foundation blue honeysuckle groups overlapped with the lower ratios observed for raspberry. Greater range in TSS and TA for the Japanese group resulted in complete overlap of the Kuril and Russian group ranges in TSS:TA. The narrow range in Kuril TSS:TA was due to low ranges in both TSS and TA. Low Japanese TSS:TA coincided with higher TSS and higher TA. High Russian TSS:TA was observed with lower TSS and lower TA. Intermediate Kuril TSS:TA resulted from moderate TA and relatively low TSS.

7.4.1.2 Improved Germplasm

The improved group ranges in DM and TSS overlapped those of their respective parental foundation groups, but the range in pH and TSS:TA for the Japanese/Russian group and the ranges in TA and TSS:TA for the Kuril/Russian group were more restricted than those of the diverse Russian group. Across the germplasm, H^2 was higher for DM, TA and TSS:TA than for pH, which was higher than for TSS (**Table 7.2**). These same patterns were seen in each improved group on its own and in the Japanese group, but the Kuril and Russian groups differed from this general pattern. Depending on the variable and improved group in question, H^2 was sometimes intermediate between that of its parental foundation groups but often higher, suggesting variability in the degree of segregation across groups. Higher h^2 was detected for TSS than for DM, while it

was negligible for TA, pH and TSS:TA across the improved germplasm. It was only considerable in the Japanese/Kuril group for DM and TA, both groups with a Japanese parent for TSS and both groups with a Kuril parent for TSS:TA, but it was negligible across groups for pH.

Overall, additive gene action was low for DM in the Japanese/Kuril group and somewhat higher for the other two groups. Transgressive segregation was high, moderate and low in the Japanese/Kuril, Japanese/Russian and Kuril/Russian groups, respectively. Dominance of Japanese DM, whether the higher or lower parent group, related to higher H^2 in this group than the other two, but overdominance was more prevalent in the former case. For TSS, despite differences in H^2 across foundation groups, additive gene action and transgressive segregation was low across all three improved groups. However, there was dominance of either higher Russian or higher Japanese TSS. Additive gene action was lower for TA in the Japanese/Kuril group than the other two groups, but transgressive segregation was high for the Japanese/Russian group and more moderate for the other groups. High and intermediate TA from the Japanese and Russian groups showed dominance and overdominance over lower TA in the Kuril group, whereas there was more overdominance than dominance of higher Japanese TA over the intermediate values seen in the Russian group. In contrast, dominance and overdominance of high Russian and low Japanese pH were observed over intermediate Kuril pH in assortive crosses, contrasting with dominance of low Japanese and overdominance of high Russian pH in the more dissortive combination. Low Japanese TSS:TA was dominant and overdominant over intermediate Kuril ratios, which were dominant and overdominant over high Russian ratios in relatively assortive crosses. For the more dissortive cross, the high Russian and low Japanese ratios showed contrasting dominance and overdominance, respectively.

7.4.2 Nutritional Content
7.4.2.1 Foundation Germplasm

The Russian group had the highest average and highest observational extremes in TP, TAC and FRAP (**Table 7.2**). The Japanese group had the lowest, and the Kuril group was intermediate. The Russian group had a broader range in TP than the Japanese group, which had a broader range than the Kuril group, but the wide range in TAC and FRAP for the Russian group contrasted in different ways with the other two groups: the Japanese group had similarly broad TAC and much narrower range in FRAP; and the Kuril group had a narrower range in TAC but an intermediate

286

range in FRAP. Relative differences between groups were similar for FW and DW calculations, which had very high absolute correlations. These findings substantiate reports for other species (Chen et al 2014) and for blue honeysuckle in specific (Kusznierewicz et al 2012; Sochor et al 2014), confirming the important role of phenolics in blue honeysuckle AOA (Rupasinghe et al 2012). Contrasting across crops, blueberry TP was relatively high and low on a FW and DW basis, respectively, and the opposite was true for strawberry. Though blueberry had high FRAP and TAC compared to raspberry and strawberry, FW and DW calculations compared differently to blue honeysuckle foundation groups for TP and compared similarly for TAC and FRAP. Correlations between TP and both measures of AOA ranged in strength from moderate to high, depending on the combination of variables and specific foundation group.

Blue honeysuckle foundation germplasm groups had ranges in TP on a FW basis that overlap the ranges for blueberry and raspberry but were higher than for strawberry. Group averages for the Japanese, Kuril and Russian groups were lower, similar and higher, respectively, than the blueberry and raspberry averages. On a DW basis, TP overlapped the ranges of all three comparison crops, while the Japanese group and blueberry averages were similar, as were the Kuril group and raspberry and strawberry averages. However, the Russian group average was much higher than for any comparison crop. As for TP, the range in blue honeysuckle TAC overlapped the blueberry and raspberry ranges but only the upper strawberry extreme on a FW basis, and it overlapped all three comparison crops on a DW basis. On a FW basis, the Japanese group and blueberry cultivars had similar averages, as for the Kuril and Russian groups and raspberry cultivars, but the strawberry average was somewhat lower. On a DW basis, averages were similar for the Japanese group and strawberry cultivars, but the blueberry and raspberry averages were lower and higher than the Kuril and Russian group averages, respectively. For FRAP, blue honeysuckle overlapped only the upper blueberry and raspberry ranges on a FW basis but overlapped their entire ranges on a DW basis; They did not overlap the lower strawberry range. Averages were higher for the Kuril and Russian groups, roughly similar for the Japanese group and the blueberry and raspberry cultivars and considerably lower for the strawberry cultivars.

7.4.2.2 Improved Germplasm

For TP, TAC and FRAP, the absolute range of observations for each of the three improved groups was greater than the range seen in any of the foundation groups (**Table 7.2**). The upper

and lower extremes in each improved group overlapped those of their respective parental foundation groups in almost all cases. Across the foundation and improved germplasm, H^2 and h^2 were negligible for TP; H^2 was slightly higher for FRAP than for TAC, though still very low; and h^2 was only noteworthy for FRAP. Further, H^2 was not remarkable for any foundation group on its own. The foundation groups compared similarly for TP, for which there was negligible H^2, but there was more variation and notable H^2 in TAC and FRAP for the Japanese/Russian and Kuril/Russian groups.

There was little transgressive segregation across improved groups, but there was more for TP than for TAC and FRAP. Also, transgressive segregation was higher on a FW than DW basis for TP, but these different calculations did not contrast for TAC and FRAP. Overall, the Japanese/Kuril group showed dominance and overdominance of lower TP, whereas the Japanese/Russian and Kuril/Russian groups showed dominance and overdominance of higher TP. The Japanese/Kuril group showed dominance of lower FRAP, but not TAC, and overdominance of both lower TAC and FRAP. In contrast, the Japanese/Russian group showed dominance of higher TAC and lower FRAP and overdominance of lower TAC and FRAP, while the Kuril/Russian group showed primarily intermediate types for TAC and little skew for FRAP.

7.5 Scientific Advancements

The current study is the first to simultaneously quantify phenological, morphological and biochemical diversity for three important blue honeysuckle foundation germplasm groups and to evaluate heritability and modes of gene action in three improved germplasm groups. It is the most comprehensive study employing biological replication, direct comparison to large-scale commercial crops and multiple years and locations in a major fruit production region with a temperate climate. The findings of this study provide strong evidence in support of the hypothesis that blue honeysuckle can be developed from a niche crop into a commercial crop with large-scale production and marketing potential.

7.5.1   Phenological Adaptation to Temperate Climates

Blue honeysuckle has phenological adaptation to a temperate climate. Though temperate climate adaptation is limited in the Russian germplasm, the intermediate Japanese and later Kuril spring phenology provide an adequate degree of temperate climate adaptation to facilitate

commercial production. Differences in spring phenological progression between foundation groups should permit selection for later bud break and bloom in tandem with both earlier and later harvest periods to simultaneously enhance the pollination period and extend the harvest season. Additive gene action between phenological extremes, moderation of these extremes by the Japanese group's intermediate phenology through dominant and overdominant gene action and high H^2 will permit selection for enhanced adaptation in improved groups. Long-term genetic gains are most feasible for the Japanese/Kuril group, especially in bloom phenology.

Northern latitudinal adaptation results in early floral initiation, which presents an indirect limitation to production in more southern latitudes due to secondary flowering. Also, early leaf drop indirectly limits production due to correlation with poor adaptation to high chill environments, but skew toward later leaf drop in improved groups shows that development of better adaptation to southern latitudes is attainable.

7.5.2   Morphological Traits Related to Agronomic Potential

Blue honeysuckle has morphological features contributing to commercial potential. The Japanese and Kuril groups are sources of greater fruit yield, weight and width, while the Japanese and Russian groups are both sources of greater fruit length. The genetic differences in fruit weight, length and width between groups are complex but are understood in relation to relative degrees of elongation and apparent density. Across the germplasm, fruit weight is a primary driver of yield, and it is more closely associated with width than length. However, within foundation groups, fruit weight has a stronger correlation with fruit length, and there are complex relationships between size parameters that vary across groups. H^2 and h^2 vary across morphological traits and across germplasm sources, suggesting opportunities to utilize variability from different sources to increase agronomic potential through hybridization. Equally, mode of gene action for fruit morphological traits was complex and varied depending on the specific trait and combination of parental foundation groups, but there are opportunities to improve agronomic potential by utilizing these differences in crossing strategies.

The anatomical basis for diversity in blue honeysuckle fruit shape provides a starting point to use specific foundation groups to develop unique fruit shapes destined for specialty markets as well as uniform, homogenous fruit shapes that are well-suited to large-scale production and mainstream marketing. The improved groups present diversities in fruit shape that were generally

expected based on the parental foundation groups. However, the diversity of combinations and relative proportions of fruit shapes across the foundation and improved germplasm, between and within germplasm groups and even within harvests of individual genotypes is evidence for polygenic control.

Oblong, ovate and cylindrical shapes are the most widespread and are commonly associated in both the foundation and improved germplasm. Rounder oblong shapes and more truncate cylindrical shapes are the most important basic fruit shapes while ovate shapes are a transitional intermediate. Beyond these three universal shapes, associations between additional fruit shapes showed consistent relationships based on their detailed anatomical descriptions. That is, modifications to the basic fruit shapes relate to variations in the environmental and nutritional factors that have direct effects on the processes of fruit development, leading to heterogeneity in both fruit shape and size within genotypes. In summary, blue honeysuckle fruit shape varies most importantly in relation to modifications in three aspects of the fruit's morphology: the length of the accessory layer relative to the fruit within, the distribution of the fruit within, the accessory layer and the way the accessory layer terminates at the distal end. The latter relates to the proximity of the accessory layer to the fruit tissue, size of the distal opening and presence or absence of a rolled accessory edge.

For each qualitative measure of agronomic potential, characterization of foundation genotypes demonstrates the existence one or more sources of either an adequate average rating or sufficient variation to permit selection of appropriate parent material for crop improvement. Combining these traits in improved germplasm will rely on the use of all three foundation groups. Selection of optimal foundation group combinations based on the specific findings of this study will facilitate generation of useful variability from which to select for improved agronomic potential and production efficiency. Generating improved genotypes with enhancements compared to the foundation germplasm can be used to overcome the morphological barriers to commercial production. In general, H^2 was high for almost all qualitative measures of agronomic potential in the improved groups. Some traits showed similarly high H^2 for all three improved groups, other traits showed lower H^2 for one group than the others and the remaining traits had relatively high, intermediate and low H^2 across the three improved groups. Also, h^2 varied across improved groups as well as traits, suggesting specific strategies for making long-term genetic gains in most traits. Overall, combination of Kuril germplasm with the Japanese and Russian germplasm

produced the best and worst average agronomic potential, respectively, while the Japanese and Russian germplasm demonstrated intermediate value for crop development. Variability in agronomic potential in the Japanese and Russian groups consistently overrides the poor contributions from the Kuril group, permitting use of this group as a source of late phenology.

7.5.3 Biochemical Traits Related to Fruit Quality and Potential Human Health Benefits

Blue honeysuckle has biochemical diversity associated with commercially marketable FQ and considerable potential human health benefits. Biochemical determinations of FQ varied across blue honeysuckle foundation groups, which provides a starting point for accessing genetic variability for breeding toward multiple objectives. There was very little diversity for each trait in the Kuril group. The Russian group had greater variability in DM than the Japanese group, but the opposite was seen for TSS:TA, and they had similar diversity in TSS, TA and pH. Of central importance to commercial marketability, blue honeysuckle possesses important variability in TSS:TA, meaning that overly tart fruit tastes are not an absolute limitation to either widespread fresh or processed consumption. The Japanese group had low TSS:TA despite high TSS, and the Russian group had high TSS:TA despite low TSS, suggesting that diversity in TSS:TA across the foundation germplasm is more directly related to differences in TA than TSS. Therefore, designing strategies to decrease TA will be more effective in improving TSS:TA.

While all combinations of foundation groups generate broad ranges in DM and TSS in even modest improved population sizes, generating as much diversity in pH, TA or TSS:TA may require larger populations. More generally, differences in H^2 and h^2 across FQ traits, as well as between and within foundation and improved groups, can be used to enhance FQ using wide-cross breeding strategies. FQ traits had higher H^2 in improved groups that had a high H^2 Japanese parent group than in combination of the Kuril and Russian groups for which H^2 was low or negligible. While TSS combined similarly across improved groups, DM, TA, pH and TSS:TA combined in different ways across improved groups, which depended on the relative differences between foundation groups and various modes of gene action. This presents opportunities for directing trait-specific crossing strategies for improving FQ. Importantly, intense selection pressure will be required to decrease TA in improved populations, but this will likely be the most effective way to increase TSS:TA due to the strong correlation between TSS:TA and TA.

The Russian group had higher average and extreme observations for TP and measures of AOA compared to the low Japanese and intermediate Kuril groups, but the degree of overlap between these groups varied across nutritional content traits. Despite strong correlations between FW and DW calculations of each trait, differences in the strength of these correlations depended on the group and trait in question, suggesting complex genetic relationships between these measures of nutritional content and morphological features such as fruit shape and size. These influence the ratio between surface area and volume as well as DM and juice content. Compared to other studies that found TP and AOA values two or three times that of other crops, the more modest findings in nutritional content of the current study have important inference for the potential human health benefits of the blue honeysuckle and its marketability as a "superfruit".

Nutritional content in improved groups showed broad ranges compared with the foundation groups, but the degree to which they overlapped depended on the variable, the specific improved group and whether values were calculated on a FW or DW basis. Relatively low H^2 implies breeding for increased nutritional content will require generation of large seedling populations with intensive phenotyping. Further, TP and measures of AOA combined in disparate ways with different modes of gene action across traits and combinations of foundation groups. Nonetheless, in each case, there is potential to improve upon each measure of nutritional content using strategic selection of parent material.

7.6 Practical Applications and Future Work

These germplasm evaluations provide fundamental information on genetic diversity and control of traits. This will facilitate development into a large-scale commercial crop by pushing the boundaries of temperate climate adaptation, agronomic potential, FQ and nutritional content in several strategic ways:

- Direct trait-specific breeding: 1) Leveraging diversity within and between foundation groups to focus crossing and selection practices; 2) Using differences in H^2 to increase breeding efficiency; 3) Utilizing additive gene action to make long-term genetic gains by concentrating desirable alleles in advanced breeding populations; and 4) Employing dominant and overdominant gene action to produce wide-cross cultivars.
- Enhance foundation group gene pools: 1) Applying selection to enhance the considerable agronomic potential and FQ in the Japanese group, especially by reducing TA and increasing

TP and AOA; 2) Obtaining greater genetic diversity in Kuril germplasm and applying selection against limiting fruit morphological features related to poor agronomic performance, especially aspects of harvestability; and 3) Selecting Russian seedlings in a temperate climate to break genetic linkage between poor phenological adaptation and desirable morphological and biochemical traits to facilitate their introgression into improved groups through hybridization.

- Utilize improved groups to advance the genetic base for the crop: 1) Continuing to generate wide-cross hybrids between enhanced foundation groups to utilize dominant and overdominant gene action that result from combination of disparate phenotypic groups; 2) Performing crosses between first generation improved populations and foundation groups (e.g., Kuril/Russian x Japanese) to recombine introgressed traits from the Russian group with the best sources of temperate climate adaptation in the Japanese and Kuril groups; 3) Making second generation crosses between improved groups (e.g., Japanese/Kuril x Japanese/Russian) to generate new diversity and transgressive segregants; and 4) Intercrossing within improved populations (e.g., Japanese/Kuril x Japanese/Kuril) to evaluate recombination between disparate genetic resources.

- Expand the range of inference for this fundamental work: 1) Evaluating the potential for additive gains in foundation groups to direct population improvement followed by subsequent wide crosses to generate first generation hybrid cultivars; 2) Pushing evaluations to more southern latitudes to expand the potential production range for the crop; 3) Utilizing information on the diversity and complexity of important morphological traits to direct development of cultivar-specific advanced horticultural methods that will increase production efficiency; and 4) Employing knowledge of FQ and nutritional content to enhance harvesting and sorting practices as well as to adapt storage technologies for fresh markets or processing protocols for value-added markets.

293

8. LITERATURE CITED

Acquaah, G (2007) Principles of Plant Genetics and Breeding, Blackwell Publishing, Malden, USA, p 283.

Ancos B, Gonzales E, Cano MP (1999) Differentiation of raspberry varieties according to anthocyanin composition. Z. Lebensm. Unters. Forsch. 208: 33.

Ancu I, Mladin G, Mladin P, Ancu S (2011) Evaluation of fruit quality at fruit selections valuable of blue honeysuckle (*Lonicera caerulea* var. *kamtschatica*). Scientific papers, R.I.F.G. Pitesti 27: 1-6.

Anikina EV, Vereshchagin AL, Syrchina AI, Larin MF, Semenov AA (1989) Citric acid esters from fruit of *Lonicera caerulea*, Plenum Publishing Corporation, New York, USA, pp 513-514.

Arber EAN (1903) On the Synanthy in the Genus Lonicera. Journal of the Linnean Society of London, Botany 35(246): 463-474.

Ashimov RR, Fefleov VA, and Igoshina VG (2009) Anomalies it is flowering and floscules in the honeysuckle. Proceedings of the 1st Virtual International Scientific Conference on *Lonicera caerulea* L.: 9-12.

Bakowska-Barczak AM, Marianchuk M, Kolodziejczyk P (2007) Survey of bioactive components in western Canadian berries. Can. J. Physiol. Pharmacol. 85: 1139-1152.

Bates D, Maechler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67(1): 1-48.

BC Ministry of Agriculture (2010) 2009-2010 Berry Production Guide for Commercial Growers, Lower Mainland Horticulture Improvement Association, Abbotsford, Canada, p 79.

Belosohov FG (2010) Study of growth dynamics of fruiting wood and yield in blue honeysuckle. Scientific and Technological Agri-Business 8: 28-30.

Belosohov FG, Belosohova OA (2011) Method of determining the blue honeysuckle fruit ripening based on analysis of changes in biochemical composition. Science Series 9(104): 203-208.

Benzie IFF, Strain JJ (1996) The ferric reducing ability of plasma (FRAP) as a measure of "antioxidant power": the FRAP assay. Analytical Biochemistry 239: 70-76.

Bertrand RA (1991) Soil management handbook for the lower Fraser Valley, British Columbia Ministry of Agriculture, Fisheries and Food, Abbotsford, Canada, p 22-32.

Bonarska-Kujawa D, Pruchnik H, Cyboran S, Żyłka R, Oszmiański J, Kleszczyńska H (2014) Biophysical mechanism of the protective effect of blue honeysuckle (*Lonicera caerulea* L. var. *kamtschatica* Sevast.) polyphenols extracts against lipid peroxidation of erythrocyte and lipid membranes. J. Membrane. Biol. 247: 611-625.

Bors B (2009) Breeding of *Lonicera caerulea* L. for Saskatchewan and Canada. Proceedings of the 1st Virtual International Scientific Conference on *Lonicera caerulea* L.: 88-98.

Bors B, Thomson J, Sander T, Oster V, Sawatzky R, Matthews L, McArthur ML, Kaban T, Treloar J, Ouellet J, Kalcits L (2009) Haskap breeding and production, Final report to Saskatchewan Agriculture, Agriculture Development Fund, Regina, Canada, http://www.agriculture.gov.sk.ca/apps/adf/ADFAdminReport/20060140.pdf Retrieved 06-01-2016

Bors B, Thomson J, Sawchuk E, Reimer P, Sawatzky R, Sander T, Kaban T, Gerbrandt E, Dawson J (2012) Haskap breeding and production, Final report to Saskatchewan Agriculture, Agriculture Development Fund, Regina, Canada, http://www.agriculture.gov.sk.ca/apps/adf/ADFAdminReport/20080042.pdf Retrieved 06-01-2016

Bors B, Sawchuk E, Dawson J, Sawatzky R (2015) Breeding and selecting haskap for nutraceutical and agronomic suitability, Final report to Saskatchewan Agriculture, Agriculture Development Fund, Regina, Canada, pp 60 http://www.agriculture.gov.sk.ca/apps/adf/ADFAdminReport/20110039.pdf Retrieved 06-01-2016

Bozek M, Wieniarska J (2006) Blooming biology and sugar efficiency of two cultivars of *Lonicera kamtschatica* (Sevast.) Pojark. Acta Agrobotanica 59(1): 177-182.

British Columbia Agri-Food Industry: Year in Review (2015) British Columbia Ministry of Agriculture, Victoria, BC, pp 1-16.

Bryksin DM (2009a) Application of growth bioregulators for increase and economical expediency of production of honeysuckle soft-wood cuttings. Proceedings of the 1st Virtual International Scientific Conference on *Lonicera caerulea* L.: 204-209.

Bryksin DM (2009b) Stages of honeysuckle development at I.V. Michirin All-Russian Research Institute of Horticulture. Proceedings of the 1st Virtual International Scientific Conference on *Lonicera caerulea* L.: 150-151.

Bryksin DM (2009c) Agronomic and biological characteristic of honeysuckle samples bred at I.V. Michirin All-Russian Research Institute of Horticulture and Frown in Central Chernozem Zone. Proceedings of the 1st Virtual International Scientific Conference on *Lonicera caerulea* L.: 99-101

Buenger J, Ackermann H, Jentzsch A, Mhling A, Pfitzner I, Reiffen KA, Schroeder KR, Wollenweber U (2006) An interlaboratory comparison of methods used to assess antioxidant potentials. Int. J. Cosmet. Sci. 28: 135-146.

Canada's Food Guide (2011) Health Canada, Ottawa, Canada, pp. 1-6.

Cantwell M (2014) Postharvest quality considerations for caneberries – blackberries, Caneberry Production Meeting, UC Hansen Ag Centre, Ventura, USA.

Celli GB, Ghanem A, Brooks MSL (2014) Haskap berries (*Lonicera caerulea* L.) – a critical review of antioxidant capacity and health-related studies for potential value-added products. Food Bioprocess Technol. 7: 1541-1554.

Chalker-Scott L (1999) Environmental significance of anthocyanins in plant stress responses. Photochemistry and Photobiology 70(1): 1-9.

Chaovanalikit A, Thompson MM, Wrolstad RE (2004) Characterization and quantification of anthocyanins and polyphenolics in blue honeysuckle (*Lonicera caerulea* L.). J. Agric. Food Chem. 52: 848-852.

Chen L, Xin X, Yuan Q, Su D, Liu W (2014) Phytochemical properties and antioxidant capacities of various colored berries. J. Sci. Food. Agric. 94: 180-188.

Chmiel T, Abogado D, Wardencki W (2014) Optimization of capillary isotachophoretic method for determination of major macroelements in blue honeysuckle berries (*Lonicera caerulea* L.) and related products. Anal. Bioanal. Chem. 406: 4965-4986.

Clark JR, Finn CE (2006) Register of new fruit and nut cultivars. HortScience 41(5): 1001-1033.

Climate Statistics (2012) http://www.jma.go.jp Retrieved 9-10-2012

Cordenusi BR, Nascimento JRO, Lajolo FM (2003) Physico-chemical changes related to quality of five strawberry fruit cultivars during cooler storage. Food Chemistry 83: 167.

Demarchi DA (2011) The British Columbia ecoregion classification (3rd Edition), Ecosystem Information Section, Ministry of Environment, Victoria, Canada.

Diamanti J, Battino M, Mezzetti B (2011) Breeding for fruit nutritional and nutraceutical quality. In: Breeding for Fruit Quality (1st edition). Eds: Jenks MA, Bebeli PJ. John Wiley and Sons, West Sussex, UK, pp 61-79.

Dudonné S, Vitrac X, Coutière P, Woillez M, Mérillon J-M (2009) Comparative study of antioxidant properties and total phenolic content of 30 plant extracts of industrial interest using DPPH, ABTS, FRAP, SOD and ORAC assays. J. Agric. Food Chem. 57: 1768-1774.

Esichev ST (2009) The results of studies of blue honeysuckle cultivars bred in Siberian and grown on Kaluga State variety plot. Proceedings of the 1st Virtual International Scientific Conference on *Lonicera caerulea* L.: 155-157.

Ershov IV (2009) Biochemical composition of fruits of honeysuckle fruits in forest-steppe zone of Altai territory. Proceedings of the 1st Virtual International Scientific Conference on *Lonicera caerulea* L.: 172-174.

Fefelov VA (2009) Breeding of blue fruit honeysuckle in Nizhnii Novgorod. Proceedings of the 1st Virtual International Scientific Conference on *Lonicera caerulea* L.: 144-147.

Fernald ML, Kinsey AC (1943) Edible Wild Plants of Eastern North America, Idlewild Press, New York, USA, pp 344-345.

Foyer CH, Noctor G (2005) Oxidant and antioxidant signalling in plants: a re-evaluation of the concept of oxidative stress in a physiological context. Plant, Cell and Environment 28: 1056-1071.

Firsov SV (2002) Evaluation of varieties and hybrids of blue honeysuckle on adaptability to the conditions of the Northeast of the European part of Russia. PhD thesis, Northeast Regional Agricultural Research Center, Federal Agency of Scientific Organizations, Russia.

Gawroński J, Hortyński J, Kaczmarska E, Dyduch-Siemińska M, Marecki W, Witorożec A (2014) Evaluation of phenotypic and genotypic diversity of some Polish and Russian blue honeysuckle (*Lonicera caerulea* L.) cultivars and clones. Acta Sci. Pol., Hortorum Cultus 13(4): 157-169.

Ghiselli A, Serafini M, Natella F, Scaccini C (2000) Total antioxidant capacity as a tool to assess redox status: Critical view and experimental data. Free Radical Biology and Medicine 29(11): 1106-1114.

Ghosh D, Konishi T (2007) Anthocyanins and anthocyanin-rich extracts: role in diabetes and eye function. Asia Pac. J. Clin. Nutr. 16: 200–208.

Golovunin VP (2009) Honeysuckle introduction in Marii El Republic. Proceedings of the 1st Virtual International Scientific Conference on *Lonicera caerulea* L.: 152-154.

Google Maps (2016) Fraser Valley, British Columbia, Canada. https://www.google.ca/maps/ Retrieved 10-10-2016

Gould KS (2004) Nature's Swiss army knife: The diverse protective roles of anthocyanins in leaves. Journal of Biomedicine and Biotechnology 5: 314-320.

Graves S, Piepho H-P, Selzer L, Dorai-Raj S (2015) multcompView: visualizations of paired comparisons. https://CRAN.R-project.org/package=multcompView Retrieved 03-01-2015

Grizodub SM (2009) Yield of the edible honeysuckle (*Lonicera* sp.) selected forms. Krasnokutskiy Research Centre of Horticulture, Ukraine, Gardening, 62.

Gruia MI, Oprea E, Gruia I, Negoita V, Farcasanu IC (2008) The antioxidant response induced by *Lonicera caerulea* berry extracts in animals bearing experimental solid tumors. Molecules 13: 1195-1206.

Gudkovskiy VA, Kozhina LV, Balakirev AE, Nazarov YB, Zhidekhina TV (2009) Means of prolongation of the marketing of honeysuckle fruit. Proceedings of the 1st Virtual International Scientific Conference on *Lonicera caerulea* L.: 178-180.

Häkkinen S, Heinonen M, Kärenlampi S, Mykkänen H, Ruuskanen J, Törrönen R (1999) Screening of selected flavonoids and phenolic acids in 19 berries. Food Research International 32: 345-353.

Halliwell B (2012) The antioxidant paradox: less paradoxical now? British Journal of Clinical Pharmacology 75(3): 637-644.

Hayrova LN (1996) Selection estimation of the raw material of blue honeysuckle (*Lonicera* subsect. Caeruleae Rehd.). PhD Thesis, All-Russian Research Institute of Horticulture: Michurin, Michurinsk.

He J, Giusti MM (2010) Anthocyanins: natural colorants with health-promoting properties. Annu. Rev. Food Sci. Technol. 1: 163-187.

Heinrich J, Valentová K, Vacek J, Palíková I, Zatloukalová M, Kosina P, Ulrichová J, Vrbková J, Šimánek V (2013) Metabolic profile of phenolic acids and oxidative stress markers after consumption of *Lonicera caerulea* L. fruit. J. Agric. Food Chem. 61: 4526-4532.

Hou D-X (2003) Potential mechanisms of cancer chemoprevention by anthocyanins. Corr. Mol. Med. 3(2): 149-159.

Hou D-X, Fujii M, Terahara N, Yoshimoto M (2004) Molecular mechanisms behind the chemopreventive effects of anthocyanidins. Journal of Biomedicine and Biotechnology 5: 321-325.

Huang D, Ou B, Prior RL (2005) The chemistry behind antioxidant capacity assays. Journal of Agricultural and Food Chemistry 53: 1841-1856.

Il'in VS, Il'ina NA (2009) Honeysuckle breeding in south Urals. Proceedings of the 1st Virtual International Scientific Conference on *Lonicera caerulea* L.: 110-111.

Imanishi H, Takada K, Masuda K, Suzuki T, Harada T (2000) Changes in freezing tolerance and soluble sugar composition in plants and calli of *Lonicera caerulea* L. during cold acclimation. Acta Hort. (ISHS) 515: 179-184.

Jin XH, Ohgami K, Shiratori K, Suzuki Y, Koyama Y, Yoshida K, Ilieva I, Tanaka T, Onoe K, Ohno S (2006) Effects of blue honeysuckle (*Lonicera caerulea* L.) extract on lipopolysaccharide-induced inflammation *in vitro* and *in vivo*. Experimental Eye Research 82: 860-867.

Jurgoński A, Juśkiewicz J, Zduńczyk Z (2013) An anthocyanin-rich extract from Kamchatka honeysuckle increases enzymatic activity within the gut and ameliorates abnormal lipid and glucose metabolism in rats. Nutrition 29(6): 898-902.

Juríková T, Rop O, Mlček J, Sochor J, Balla S, Szekeres L, Hegedusova A, Hubalek J, Adam J, Kizek R (2012a) Phenolic profile of edible honeysuckle berries (genus *Lonicera*) and their biological effects. Molecules 17: 61-79.

Juríková J, Sochor J, Rop O, Mlček J, Balla S, Szekeres L, Žitný R, Zitka O, Adam V, Kizek R (2012b) Evaluation of polyphenolic profile and nutritional value of non-traditional fruit species in the Czech Republic – a comparative study. Molecules 17: 8968-8981.

Juríková T, Ercişli S, Rop O, Mlček J, Balla S, Zitny R, Sochor J, Hegedusova A, Benedikova D, Ďurišová L (2014) The evaluation of anthocyanin content of honeyberry (*Lonicera kamtschatica*) clones during freezing in relation to antioxidant activity and parameters of nutritional value. Zemdirbyste-Agriculture 101(2): 215-220.

Kanarsky AA, Khabarov SN, Khokhryakova LA (2013) Highlights of fitness of selections of honeysuckle for mechanical harvesting. Agriculture and Plant Cultivation Scientific and Technological Agri-Business 7: 20-21.

Katalinic V, Milos M, Kulisic T, Jukic M (2006) Screening of 70 medicinal plant extracts for antioxidant capacity and total phenols. Food Chemistry 94: 550-557.

Kelley CC, Spilsbury RH (1939) Soil survey of the lower Fraser Valley. Dominion of Canada, Department of Agriculture, Ottawa, Canada, Publication 650, Technical Bulletin 20.

Kempler C, Daubeny HA, Frey L, Walters T (2006) 'Chemainus' red raspberry. HortScience 41(5), 1364-1366.

Kempler C, Daubeny HA, Harding B, Frey L, Baumann TE, Finn CE, Khanizadeh S, Jamieson AR, MacKenzie K, Moore PP, Sweeney M (2011) 'Stolo' strawberry. HortScience 46(7), 1046-1048.

Kempler C, Daubeny HA, Harding B, Baumann T, Finn CE, Moore PP, Sweeney M, Walters T (2007) 'Saanich' red raspberry. HortScience 42(1), 176-178.

Khokhryakova LA (2004) Economic-biological estimation of breeds and perfect forms of honeysuckle in the forest-steppe zone of the Altai Territory. Ph.D. Thesis, Berry Experimental Station, Michurina, IV. Michurin, Russia.

Kim D-O, Chun OK, Kim YJ, Moon H-Y, Lee CY (2003) Quantification of polyphenolics and their antioxidant capacity in fresh plums. J. Agric. Food. Chem. 51: 6509-6515.

Kim JG, Kim HL, Kim SJ, Park K-S (2013) Fruit quality, anthocyanin and total phenolic contents, and antioxidant activities of 45 blueberry cultivars grown in Suwon, Korea. Journal of Zhejiang Univ-Sci B (Bioed and Biotechnol) 1(9): 793-799.

Kirin IB (2010) The specifics of the stages of organogenesis in the variety of honeysuckle. Agriculture and Plant Cultivation Scientific and Technological Agri-Business 8: 27-28.

Kolasin E, Pozdnyakov A (1991) Knowledge on Medicinal Fruit, Knowledge, Moscow, pp 38-59.

Korobkova TS (2009) Introduction of honeysuckle into central Yakutiya. Proceedings of the 1st Virtual International Scientific Conference on *Lonicera caerulea* L.: 158-161.

Kramers RE, Rose I, Monette J, Morisset N (2014) Plant Hardiness Zone Maps, Canada Centre for Mapping and Observation, Natural Resources Canada. http://www.planthardiness.gc.ca/ Retrieved 31-10-2016.

Krisova AY, Shelkovskaya NK, Khokhryakova LA, Borodulina ID (2012) The variability of biochemical composition of honeysuckle fruits in the Altai Territory forest-steppe zone. The news of Altai State University 3(2): 39-41.

Kuklina AG (2009) Honeysuckle culture in Russia. Proceedings of the 1st Virtual International Scientific Conference on *Lonicera caerulea* L.: 50-51.

Kuminov LP (2009) Honeysuckle breeding near Moscow. Proceedings of the 1st Virtual International Scientific Conference on *Lonicera caerulea* L.: 112-116.

Kusznierewicz B, Piekarska A, Mrugalska B, Konieczka P, Namieśnik J, Bartoszek A (2012) Phenolic composition and antioxidant properties of Polish blue-berried honeysuckle genotypes by HPLC-DAD-MS, HPLC postcolumn derivatization with ABTS or FC, and TLC with DPPH visualization. J. Agric. Food Chem. 60: 1755-1763.

Lamoureux D, Sorokin A, Lefèvre I, Alexanian S, Eyzaguirre P, Hausman J-F (2011) Investigation of genetic diversity in Russian collections of raspberry and blue honeysuckle. Plant Genetic Resources: Characterization and Utilization 9(2): 202-205.

Lau FC, Shukitt-Hale B, Joseph JA (2006) Beneficial effects of berry fruit polyphenols on neuronal and behavioural aging. J. Sci. Food. Agric. 86: 2251-2255.

Lee J, Finn CE (2007) Anthocyanins and other polyphenolics in American elderberry (*Sambucus canadensis*) and European elderberry (*S. nigra*) cultivars. Journal of the Science of Food and Agriculture 87: 2665-2675.

Lee JC, Dreves AJ, Cave AM, Kawai S, Isaacs R, Miller JC, Van Timmeren S, Bruck DJ (2015) Infestation of wild and ornamental noncrop fruits by *Drosophila suzukii* (Diptera: Drosophilidae). Annals of the Entomological Society of America 108(2): 117-129.

Li J, Li G, Wu S, Ababarri S (2009) Study on impact of black currant and *Lonicera caerulea* fruit on rabbits with hyperlipemia. Endemic Disease Bulletin 24(1): 14-16.

Lila MA (2004) Anthocyanins and human health: An *in vitro* investigative approach. Journal of Biomedicine and Biotechnology 5: 306-313.

Makarov VN, Vlazneva LN, Akim MYU, Mironov AM (2009) The development of new functional food-stuffs on the basis of honeysuckle cultivars with a high level of valuable [sic]. Proceedings of the 1st Virtual International Scientific Conference on *Lonicera caerulea* L.: 184-189.

Malodobry M, Bieniasz M, Dziedzic E (2010) Evaluation of the yield and some components in the fruit of blue honeysuckle (*Lonicera caerulea* var. *edulis* Turcz. Freyn.). Folia Horticulturae Ann. 22(1): 45-50.

Marsh K, Attanayake S, Walker S, Gunson A, Boldingh H, MacRae E (2004) Acidity and taste in kiwifruit. Postharvest Biology and Technology 32: 159-168.

Matuškovič J, Juríková T, Gazdík Z, Řezniček V (2009a) Research programs in the edible honeysuckle, their results in the conditions of Slovakia and our future intentions. Proceedings of the 1st Virtual International Scientific Conference on *Lonicera caerulea* L.: 52-60.

Matuškovič J, Juríková T, Jurík I, Šimko J, Gazdík Z (2009b) The content of anthocyanins and ascorbic acid in the gene pool of 22 clones of *Lonicera kamtschatica* (Sevast.) Pojark. Gerda 25. Agriculture 55: 88-94.

Matuškovič J, Pokorná-Juríkova T (2007) The evaluation of growth dynamics of *Lonicera kamtschatica* clones. Acta Universitatis Agriculturae et Silviculturae Mendelianae Brunensis 55(2): 53-58.

Maunder WJ (1968) Synoptic weather patterns in the Pacific Northwest. Northwest Science 42 (2): 80-88.

McKenney DW, Hutchinson MF, Kesteven JL, Venier LA (2001) Canada's plant hardiness zones revisited using modern climate interpolation techniques. Can. J. Plant Sci. 81: 129–143.

McKey D, Elias M, Pujol B, Duputié A (2010) The evolutionary ecology of clonally propagated domesticated plants. New Phytologist 186: 318-332.

Mezhenskiy VN (2009) Perspectives of the edible honeysuckle production in Ukraine. Proceedings of the 1st Virtual International Scientific Conference on *Lonicera caerulea* L.: 162-164.

Mittler R (2002) Oxidative stress, antioxidants and stress tolerance. TRENDS in Plant Science 7 (9): 405-410.

Miyashita T, Araki H, Hoshino Y (2010) Ploidy distribution and DNA content variations of *Lonicera caerulea* (Caprifoliaceae) in Japan. J Plant Res. 124(1): 1-9.

Moore PP (2007) Raspberry cultivar 'Cascade Bounty'. U.S. Patent No. US PP18,246 P3 filed February 15, 2007, and issued November 27, 2007.

Moore PP, Sjulin TM, Shanks CH (1995) 'Puget Reliance' strawberry. HortScience 30(7), 1468-1469.

Mucina L (1997) Conspectus of classes of European vegetation. Folia Geobot. Phytotax. 32: 117-172.

Murslimova GR (2013) The adaptive potential of introduced varieties of *Lonicera* L. in the steppe zone of the Southern Urals. Contemporary Horticulture 3: 1-7.

Muth ER, Laurent JM, Jasper P (2000) The effect of bilberry nutritional supplementation on night visual acuity and contrast sensitivity. Altern. Med. Rev. 5(2): 164-1172.

Nakajima F (1996) Small fruit growing in Hokkaido. Hokkaido Prefecture Agricultural Extension Services, Extension Publication, Sapporo, Japan.

Naugžemys D, Žilinskaitė S, Skridaila A, Žvingila D (2014) Phylogenetic analysis of the polymorphic 4_x species complex *Lonicera caerulea* (Caprifoliaceae) using RAPD markers and noncoding chloroplast DNA sequences. Biologia 69(5): 585-593.

Naumova LV (2009) Honeysuckle pests in Moscow region. Proceedings of the 1st Virtual International Scientific Conference on *Lonicera caerulea* L.: 197-199.

Niki E (2010) Assessment of antioxidant capacity *in vitro* and *in vivo*. Free Radical Biology and Medicine 49(4): 503-515.

Ochmian I, Grajkowski J (2007) Growth and yielding of three blue honeysuckle (*Lonicera caerulea*) cultivars in western Pomeranian in first years after planting. Annals of the Agricultural University of Poznan 383 (41): 351-355.

Ochmian I, Grajkowski J, Skupień K (2008) Field performance, fruit chemical composition and firmness under cold storage and simulated "shelf-life" conditions of three blue honeysuckle cultivars (*Lonicera caerulea*). Journal of Fruit and Ornamental Plant Research 16: 83-91.

Ochmian I, Skupień K, Grajkowski J, Smolik M, Ostrowska K (2012) Chemical composition and physical characteristics of fruits of two cultivars of blue honeysuckle (*Lonicera caerulea* L.) in relation to their degree of maturity and harvest date. Not. Bot. Horti. Agrobo. 40(1): 155-162.

Ochmian I, Smolik M, Dobrowolska A, Rozwarski R, Kozos K, Chelpinski P, Ostrowska K (2013) The influence of harvest date on fruit quality of several cultivars of blue honeysuckle berries. Electronic Journal of Polish Agricultural Universities 16 (1): Article 2.

Oszmiański J, Kucharska A, Gasiewicz E (1999) Usefulness of honeysuckle fruits for juice production. In: Fruit and vegetable juices for drinks today and in the XXI century. Eds: Michalczuk L, Plocharski W. Research Institute of Pomology and Floriculture, Rytro, Poland, pp 251-260.

Palíková I, Heinrich J, Bednář P, Marhol P, Křen V, Cvak L, Valentová K, Růžička F, Holá V, Kolář M, Šimánek V, Ulrichová J (2008) Constituents and antimicrobial properties of blue honeysuckle: A novel source for phenolic antioxidants. J. Agric. Food Chem. 56: 11883-11889.

Passam HC, Karapanos IC, Alexopoulos AA (2011) The biological basis of fruit quality. In: Breeding for Fruit Quality (1st edition). Eds: Jenks MA, Bebeli PJ. John Wiley and Sons, West Sussex, UK, pp 5-38.

Peel MC, Finlayson BL, McMahon TA (2007) Updated world map of the Köppen-Geiger climate classification. Hydrol. Earth Syst. Sci. 11: 1633-1644.

Petrushua EN (2009) The main results of honeysuckle breeding in Kamchatka Kray. Proceedings of the 1st Virtual International Scientific Conference on *Lonicera caerulea* L.: 117-121.

Plekhanova MN (1986) *Lonicera kamtchatica* (Sevast.) Pojark. on Iturup Island and prospective for its utilization. Plant Natural Resources 22: 99-106.

Plekhanova MN (1988) Descriptor for the species and varieties of *Lonicera* subsect. Caeruleae (Blue Honeysuckle). All Union Institute of Plant Breeding (VIR). Leningrad.

Plekhanova MN (1989) Actinidia, Schizandra, and Blue Honeysuckle. Leningrad, Agronomy 88.

Plekhanova MN (1992) Prospective varieties and forms of blue honeysuckle for selection and production, Bulletin of Applied Botany, Genetics, and Plant Breeding, vol. 146. Russian Academy of Agricultural Science, Leningrad, Russia.

Plekhanova MN (1994a) Blue honeysuckle: A new berry from Russia. Pomona 29(1): 46-48.

Plekhanova MN (1994b) Honeysuckle (*Lonicera* subsect. Caeruleae): systematics, biology, selection. PhD Thesis, Russian Academy of Agricultural Sciences, St. Petersburg, Russia.

Plekhanova MN (1998) Blue honeysuckle in the garden and nursery. N.I. Vavilov Research Institute of Plant Industry, Department of Fruit Crops, St. Petersburg, Russia, pp 16-58.

Plekhanova MN (2000) Blue honeysuckle (*Lonicera caerulea* L.) – A new commercial berry crop for temperate climate: Genetic resources and breeding. Acta Hort (ISHS) 538: 159-164.

Plekhanova MN, Rostova RS (1994) The analysis of variability of morphological, anatomical and biochemical characters of *Lonicera* in subsection Caeruleae (Caprifoliaceae) with the help of the method of principal components. Bot. Zhurnal 79(2): 45-64.

Plekhanova MN, Sokoleva K (1992) Systematics, initial material for breeding, biology and morphology of fruit crops. The Russian Academy of Agricultural Science, Bulletin of applied botany, genetics and plant breeding 146.

Plekhanova MN, Solovyeva LV, Mochalova OV (1992) Chromosome numbers and distribution area of *Lonicera* subsect. Caeruleae (Caprifoliaceae). Bot. Zhurnal 77(9): 1-11.

Podsędek A, Majewska I, Redzynia M, Sosnowska D, Koziołkiewicz M (2014) *In vitro* inhibitory effect on digestive enzymes and antioxidant potential of commonly consumed fruits. J. Agric. Food Chem. 62: 4610-4617.

Pojarkova AI (1958) Honeysuckle – *Lonicera*. In: Flora of the USSR: Volume 23: Bignoniaceae – Valerianaceae. Eds: Schischkin VK. Akademiya Nauk SSSR, Moscow-Leningrad, Russia, pp 446-482.

Polina SA, Efremov AA (2015) Determination of composition of anthocyanins in black chokeberry, serviceberry and blue-berried honeysuckle with HPLC. Journal of Siberian Federal University Chemistry 1:143-154.

Prior RL, Cao G (1999) *In vivo* total antioxidant capacity: Comparison of different analytical methods. Free Radical Biology and Medicine 27(11/12): 1173-1181.

Prischepina G (2000) Culture of Altai honeysuckle (*Lonicera altaica* Pall.) in the forest-steppe zone of the Altai territory. PhD Thesis, Altai State Agrarian University, Altai, Russia.

Proteggente AR, Pannala A, Paganga G, Van Buren L, Wagner E, Wiseman S, Van De Put F, Dacombe C, Rice-Evans CA (2002) The antioxidant activity of regularly consumed fruit and vegetables reflects their phenolic and vitamin C composition. Free Radical Research 36(2): 217-233.

R Development Core Team (2015) R: A language and environment for statistical computing, R Foundation for Statistical Computing, Vienna, Austria. http://www.Rproject.org Retrieved 01-01-2015

Raudsepp P, Anton D, Raosto M, Meremäe K, Pedastsaar P, Mäesaar M, Raal A, Laikoja K, Püssa T (2013) The antioxidative and antimicrobial properties of the blue honeysuckle (*Lonicera caerulea* L.), Siberian rhubarb (*Rheum rhaponticum* L.) and some other plants, compared to ascorbic acid and sodium nitrate. Food Control 31: 129-135.

Razumnikov NA, Ryabinin MI, Nikolaeva EV, Solomina EN (2009) Honeysuckle breeding in the Botanical Gardens – Institute in Marii El Republic. Proceedings of the 1st Virtual International Scientific Conference on *Lonicera caerulea* L.: 122-123.

Re R, Pellegrini N, Proteggente A, Pannala A, Yang M, Rice-Evans C (1999) Antioxidant activity applying an improved ABTS radical cation decolorization assay. Free Radical Biology & Medicine 26(9/10): 1231-1237.

Rehder A (1903) Synopsis of the genus *Lonicera*. *Annual* Report Missouri Bot. Garden 14: 28-73.

Rehder A (1909) Note on the morphology of the fruit of *Lonicera caerulea*: The fruit of *Lonicera caerulea*. Rhodora 11: 209-211.

Renata M (2001) Study of vegetative, growing and economic character of genus *Lonicera* subsect. Caeruleae REHD. Proceedings of the 9th International Conference of Horticulture: 130-135.

Renaud S, de Lorgeril M (1992): Wine, alcohol, platelets and the French paradox for coronary heart disease. Lancet 339: 1523-1526.

Řezníček V, Salaš V (2004) Gene pool of less widely spread fruit tree species. Acta Universitatis Agriculturae et Silviculturae Mendelianae Brunensis 52(4): 159-168.

Rieseberg LH, Archer MA, Wayne RK (1999) Transgressive segregation, adaptation and speciation. Heredity 83: 363-372.

Rop O, Řezníček V, Mlček J, Jurikova T, Balik J, Sochor J, Kramarova D (2011) Antioxidant and radical oxygen species scavenging activities of 12 cultivars of blue honeysuckle fruit. Hort. Sci. (Prague) 38(2): 63-70.

Rudenberg L, Green P (1969a) A karyological survey of *Lonicera*, I. Journal of the Arnold Arboretum 47: 222-229.

Rudenberg L, Green P (1969b) A karyological survey of *Lonicera*, II. Journal of the Arnold Arboretum 50: 449-451.

Rupasinghe HPV, Yu LJ, Bhullar KS, Bors B (2012) Short communication: Haskap (*Lonicera caerulea*): A new berry crop with high antioxidant capacity. Can. J. Plant Sci. 92: 1311-1317.

Rupasova ZA, Garanovich IM, Vasilevskaya TI, Varavina NP, Shpitalnaya TV (2009) Peculiarities of biochemical composition of the edible honeysuckle fruit (*Lonicera edulis*

Turcz. ex Freyn) in Belarus. Proceedings of the 1st Virtual International Scientific Conference on *Lonicera caerulea* L.: 175-177.

Ryabinina ML (2009) Collection of blue fruited honeysuckle in the Botanical Gardens of Komi Institute of Biology. Proceedings of the 1st Virtual International Scientific Conference on *Lonicera caerulea* L.: 69-72.

Ryabnickova E (2011) Kamchatka Honeysuckle – unconventional fruit of the Czech Republic. Undergraduate Thesis, Faculty of Chemistry, Technical University of Brno, Czech Republic.

Sabitov A (1986) Species of blue fruited honeysuckle, prospects for breeding. All Union Order of Lenin and Order of Friends of Nature Science Research Institute of Plant Growing, Leningrad, Russia.

Saftner R, Polashock J, Ehlenfeldt M, Vinyard B (2008) Instrumental and sensory quality characteristics of blueberry fruit from twelve cultivars. Postharvest Biology and Technology 49: 19-26.

Sarja L (1998) Honeysuckle with edible berries. National Botanical Gardens of Latvia, Salaspils, Latvia.

Sabitov A, Chebukin P, Hummer KE (2007) Plant exploration for fruit genetic resources in Sakhalin territory. Acta Hort. 760: 381-388.

Savinich EA (2015) Biological-industrial evaluation of honeysuckle in conditions of Krasnoyarsk forest-steppe. Proceedings of Regional Scientific and Practical Student International Conference, Ministry of Agriculture of the Russian Federation, Irkutsk State Agrarian University 2: 69-72.

Savinkova NV, Gagarkin AV (2009) Honeysuckle culture on Bakchar supporting point of the northern horticulture, stages of activity and some results. Proceedings of the 1st Virtual International Scientific Conference on *Lonicera caerulea* L.: 129-137.

Sedlák J, Paprštein F (2007) *In vitro* propagation of blue honeysuckle. Hort. Sci. 34(4): 129-131.

Shamaila M, Baumann TE, Eaton GW, Powrie WD, Skura BJ (1992) Quality attributes of strawberry cultivars grown in British Columbia. Journal of Food Science 57(3): 696-700.

Shchekotova EA (2009) Increase in honeysuckle precocity. Proceedings of the 1st Virtual International Scientific Conference on *Lonicera caerulea* L.: 84-87.

Sheyko VV (2009) Honeysuckle response (*Lonicera caerulea* L.) to excessively wet and cold temperate climate. Proceedings of the 1st Virtual International Scientific Conference on *Lonicera caerulea* L.: 75-83.

Shimoyama Y (2008) The Hascup: an introduction, Agricultural Affairs Division, Department of Industrial Promotion, Hokkaido, Japan, pp 1-14.

Shukitt-Hale B, Lau FC, Joseph JA (2008) Berry fruit supplementation and the aging brain. J. Agric. Food Chem. 56: 636-641.

Singleton V, Orthofer R, Lamuela-Raventós RM (1999) Analysis of total phenols and other oxidation substrates and antioxidants by means of folin-ciocalteu reagent. Meth. Enzym. 299: 152-178.

Skvortsov AK (1986) Blue honeysuckle (*Lonicera* subsect. Caeruleae) of Eurasia: Distribution, taxonomy, chromosome numbers, domestication. Acta Univ. Ups. Symb. Bot. Ups. 27(2): 95-105.

Sochor J, Jurikova T, Pohanka M, Skutkova H, Baron M, Tomaskova L, Balla S, Klejdus B, Pokluda R, Mlček J, Trojakova Z, Saloun J (2014) Evaluation of antioxidant activity, phenolic compounds, amino acids and mineral elements of representative genotypes of *Lonicera edulis*. Molecules 19: 6505-6523.

Sorokin AA (2002) Improvement of methods of seed and vegetative propagation of blue honeysuckle. PhD thesis, National Agrarian University, St. Petersburg, Russia.

Stepanova NN (2009) Honeysuckle culture in Priamurye. Proceedings of the 1st Virtual International Scientific Conference on *Lonicera caerulea* L.: 138-143.

Stintzing FC, Carle R (2004) Functional properties of anthocyanins and betalins in plants, food and in human nutrition. Trends in Food Science & Technology 15: 19-38.

Suchkova SA, Senina EG (2009) Studies on honeysuckle cultivars in Tomsk region. Proceedings of the 1st Virtual International Scientific Conference on *Lonicera caerulea* L.: 165-168.

Suzuki T, Uenohata M, Oosawa K (2007) Polyploidy breeding of blue honeysuckle and black chokeberry by utilizing *in vitro*-cultures treated with colchicine. Proceedings of the Second International Symposium on Plant Genetic Resources of Horticultural Crops 1-2, Acta Hort 760: 389-396.

Svobodová A, Ramdousková J, Walterová D, Vostálová J (2008) Protective effects of phenolic fraction of blue honeysuckle fruits against UVA-induced damage to human keratinocytes. Arch. Dermatol. Res. 300: 225-233.

Szot I, Lipa T (2012) Influence of betokson super and fertilizers on chemical composition of fruits and leaves of blue honeysuckles. Acta Sci. Pol., Hortotum Cultus 11(5): 113-125.

Takada M, Nakano H, Hoshino Y, Sato H (2003) Evaluation of eating qualities and some horticultural characteristics for selection of elite lines in *Lonicera caerulea* L. Research Bull. Hokkaido Univ. Farm 33: 21-38.

Tanaka S, Karizaki M, Watanabe H, Minegishi T, Matsui F, Muramatsu H, Ogano R, Narita H, Iwasaki A (1994) New blue honeysuckle (*Lonicera caerulea* L. var. *emphyllocalyx* Nakai) cultivar 'Yufutsu'. The Bulletin of Hokkaido Prefectural Agricultural Experiment Stations 67: 29-41.

Tanaka T, Tanaka A (1998) Chemical composition and characteristics of hasukappu berries in various cultivars and strains. J. Jap. Soc. Food Sci. and Tech. 45(2): 129-133.

Tang Z, Zang S, Zhang X (2012) Detection of chlorogenic acid in honeysuckle using infrared-assisted extraction followed by capillary electrophoresis with UV detector. Journal of Chromatographic Science 50: 76-80.

Teplyuk HY (2000) Ecological features blue honeysuckle in the southern part of the Krasnoyarsk territory. PhD thesis, Krasnoyarsk, Russia.

Terahara N, Sakanashi T, Tsukui A (1993) Anthocyanins from the berries of haskaap, *Lonicera caerulea* L. J. Home Econ. Jpn. 44(3): 197-201.

Thaipong K, Booprakob U, Crosby K, Cisneros-Zevallos L, Byrne DH (2006) Comparison of ABTS, DPPH, FRAP, and ORAC assays for estimating antioxidant activity from guava fruit extracts. Journal of Food Composition and Analysis 19(6-7): 669-675.

The Weather Network (2015) Historical weather, British Columbia. www.theweathernetwork.com/ca/weather/historical-weather/ Retrieved 08-01-2015

Thomas MJ (2000) The role of free radicals and antioxidants. Nutrition 16(7-8): 716-718.

Thompson MM (2006a) Introducing Haskap, the Japanese blue honeysuckle. J. Amer. Pomol. Soc. 60:164-168.

Thompson MM (2006b) Haskap arrives in North America. Pome. New. 31(3): 65-69.

Thompson MM (2016) U.S. Patent No. US PP26,642 P2 filed August 14, 2014, and issued April 26, 2016.

Thompson MM, Barney DL (2007) Evaluation and breeding of Haskap in North America. J. Amer. Pomol. Soc. 61(1): 25-33.

Thompson MM, Chaovanalikit A (2003) Preliminary observations on adaptation and nutraceutical values of blue honeysuckle (*Lonicera caerulea*) in Oregon, USA. Acta Hort. (ISHS) 626: 65-72.

Tomankova K, Kolarova H, Pizova K, Binder S, Konecny P, Kriegova E, Malina L, Horakova J, Malohlava J, Kejlova K, Jirova D (2014) Cytotoxicity and antioxidative effects of herbal and fruit extracts *in vitro*. Food Biophysics 9: 267-276.

Truta E, Vochita G, Rosu CM, Zamfirache MM, Olteanu Z, Oprica L (2013) Karyotype traits in Romanian selections of edible blue honeysuckle. Turk. J. Biol. 31: 60-68.

Tsuda T (2008) Regulation of adipocyte function by anthocyanins: possibility of preventing the metabolic syndrome. J. Agric. Food Chem. 56(3): 642–46.

Ulrich D, Olbricht K (2011) Fruit organoleptic properties and potential for their genetic improvement. In: Breeding for fruit quality (1st edition). Eds: Jenks MA, Bebeli PJ. John Wiley and Sons, West Sussex, UK, pp 41-59.

Velioglu YS, Mazza G, Gao L, Oomah BD (1998) Antioxidant activity and total phenolics in selected fruits, vegetables, and grain products. J. Agric. Food Chem. 46: 4113-4117.

Wojdyło A, Jáuregui PNN, Carbonell-Barrachina AA, Oszmiański J, Golis T (2013) Variability of phytochemical properties and content of bioactive compounds in *Lonicera caerulea* L. var. *kamtschatica* berries. J. Agric. Food Chem 61: 12072-12082.

Wong SP, Leong LP, Koh JHW (2006) Antioxidant activities of aqueous extracts of selected plants. Food Chemistry 99: 775-783.

Wu XJ (1997) Characterization of florescence, fructification, pollination and fertilization of blue honeysuckle (*Lonicera caerulea* L.). MSc Thesis. Northeast Agricultural University.

Wu X, Gu L, Prior RL, McKay S (2004) Characterization of anthocyanins and proanthocyanidins in some cultivars of *Ribes, Aronia*, and *Sambucus* and their antioxidant capacity. J. Agric. Food Chem. 52: 7846-7856.

Wu S, He X, Qin S, He J, Zhang S, Hou D-X (2015) Inhibitory effects of blue honeysuckle (*Lonicera caerulea* L.) on adjuvant-induced arthritis in rats: crosstalk of anti-inflammatory and antioxidant effects. Journal of Functional Foods 17: 514-523.

Yahia EM (2010) The contribution of fruit and vegetable consumption to human health. In: Fruit and vegetable phytochemicals: chemistry, nutritional value and stability. Eds. de la Rosa LA, Alvarez-Parrilla E, Gonzalez-Aguilar GA. Blackwell Publishing, Ames, Iowa, pp 3-51.

Zadernowski R, Naczk M, Nesterowicz J (2005) Phenolic acid profiles in some small berries. J. Agric. Food Chem. 53: 2118-2124.

Zhidyokhina TV (2009) The method of estimation of photosynthetic activity of honeysuckle leaves during fruit development. Proceedings of the 1st Virtual International Scientific Conference on *Lonicera caerulea* L.: 31-36.

Zholobova ZP, Khokhryakova LA (2009) Means and the results of honeysuckle breeding in Altai. Proceedings of the 1st Virtual International Scientific Conference on *Lonicera caerulea* L.: 102-109.

Žilinskaitė S, Naugžemys D, Radaitienė D, Žvingila D (2007) Investigation of blue-berries honeysuckle lines and cultivars in Vilnius University Botanical Garden collection. Scientific works of the Lithuanian Institute of Horticulture and Lithuanian University of Agriculture 26(3): 47-56.

Zulueta A, Esteve MJ, Frígola A (2009) ORAC and TEAC assays comparison to measure the antioxidant capacity of food products. Food Chemistry 114: 310-316.

9. APPENDICES

9.1 Appendix A

Appendix A.1. Male and female parental foundation blue honeysuckle genotypes used to produce 40 improved hybrid families selected from the U of S breeding program for evaluation in 2012/2013 in the Fraser Valley, BC, Canada (J – Japanese, K – Kuril, R – Russian, JK and KJ – Japanese/Kuril, JR and RJ – Japanese/Russian, KR and RK – Kuril/Russian).

	Family	Female Parent	Male Parent		Family	Female Parent	Male Parent
Japanese/ Kuril	JK-GH17	MT-41-83	SX-3-07	Japanese/ Kuril	KJ-GH1	SX-3-03	MT-43-87
	JK-GH18	MT-42-45	SX-3-07		KJ-GH3	SX-97-12	MT-43-87
	JK-GH19	MT-43-87	SX-3-07		KJ-GH2	SX-97-12	MT-46-55
	JK-GH10	MT-45-14	SX-3-07				
	JK-GH4	MT-56-18	SX-3-07				
Japanese/ Russian	JR-100	MT-21-78	MT-27-35	Kuril/ Russian	KR-KR7	SX-3-06	SX-2-11
	JR-GH11	MT-444-39	SX-2-16		KR-KR5	SX-3-06	SX-2-13
	JR-GH5	MT-56-18	SX-2-16		KR-2	SX-3-06	SX-2-13
	JR-GH18	MT-41-83	SX-2-06		KR-KR11	SX-3-06	SX-2-06
	JR-GH14	MT-66-53	SX-2-16		KR-7-10	SX-3-03	SX-2-10
	JR-GH25	MT-73-39	SX-2-16		KR-7-12	SX-3-03	SX-2-13
	JR-GH22	MT-22-14	SX-2-06		KR-7-14	SX-3-03	SX-2-16
	JR-GH23	MT-43-87	SX-2-06		KR-7-13	SX-3-03	SX-2-14
	RJ-J2	SX-2-07	MT-66-53		RK-T12	SX-2-16	SX-3-06
	RJ-B7	SX-2-13	MT-66-53		RK-V6	SX-2-06	SX-3-05
	RJ-B2	SX-2-10	MT-73-39		RK-R6	SX-2-06	SX-3-06
	RJ-J7	SX-2-13	MT-41-83		RK-V12	SX-2-11	SX-97-12
	RJ-T9	SX-2-16	MT-73-39		RK-T18	SX-2-11	SX-3-05
	RJ-V4	SX-2-06	MT-444-39		RK-V18	SX-2-16	SX-3-07
	RJ-B9	SX-2-13	MT-56-18		RK-T6	SX-2-14	SX-97-12
	RJ-J4	SX-2-07	MT-444-39		RK-R12	SX-2-07	SX-3-07
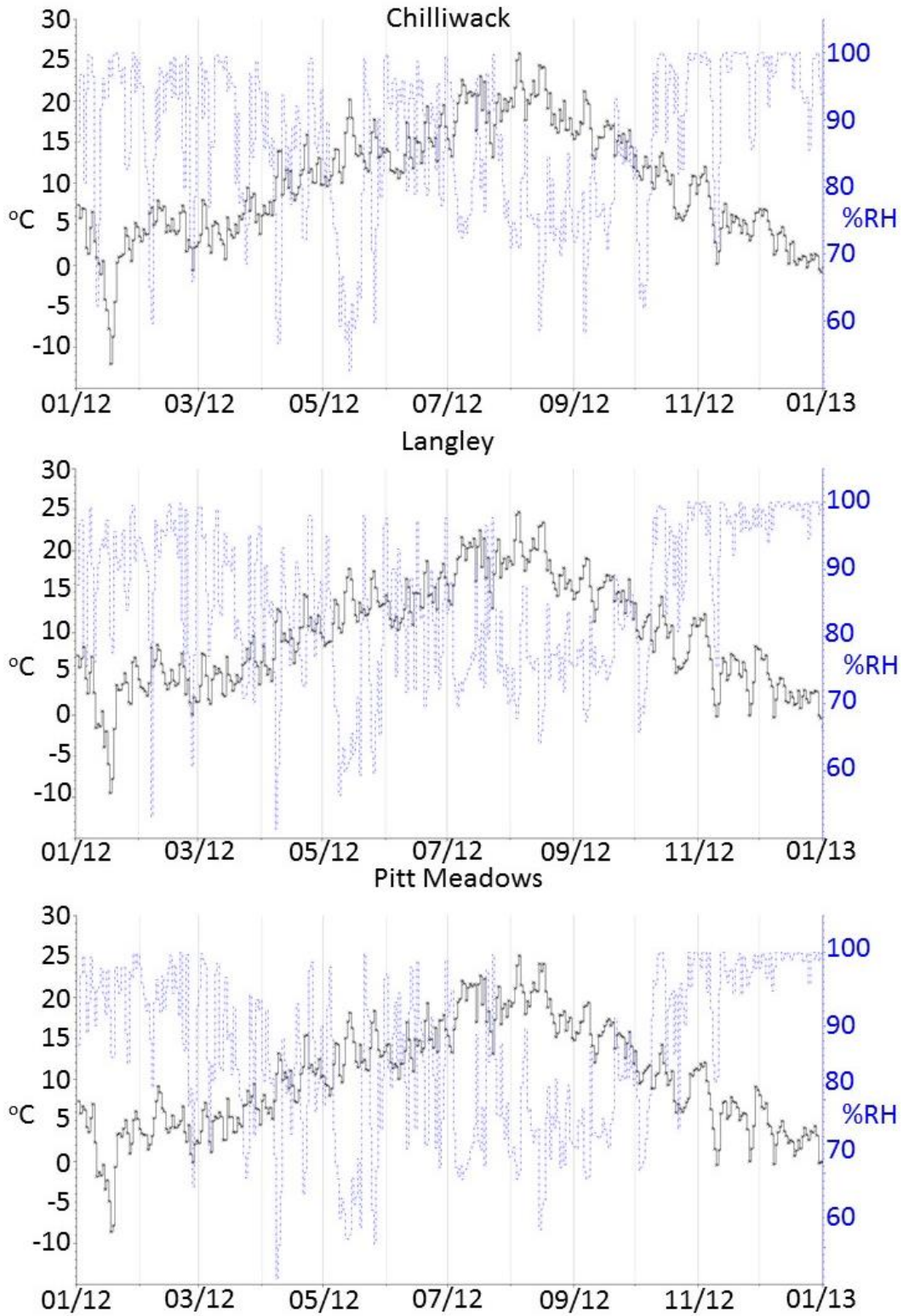
Appendix A.2. Average daily temperature and relative humidity for three trial sites in the Fraser Valley, BC, Canada in 2012 (black line – temperature, blue line – relative humidity).
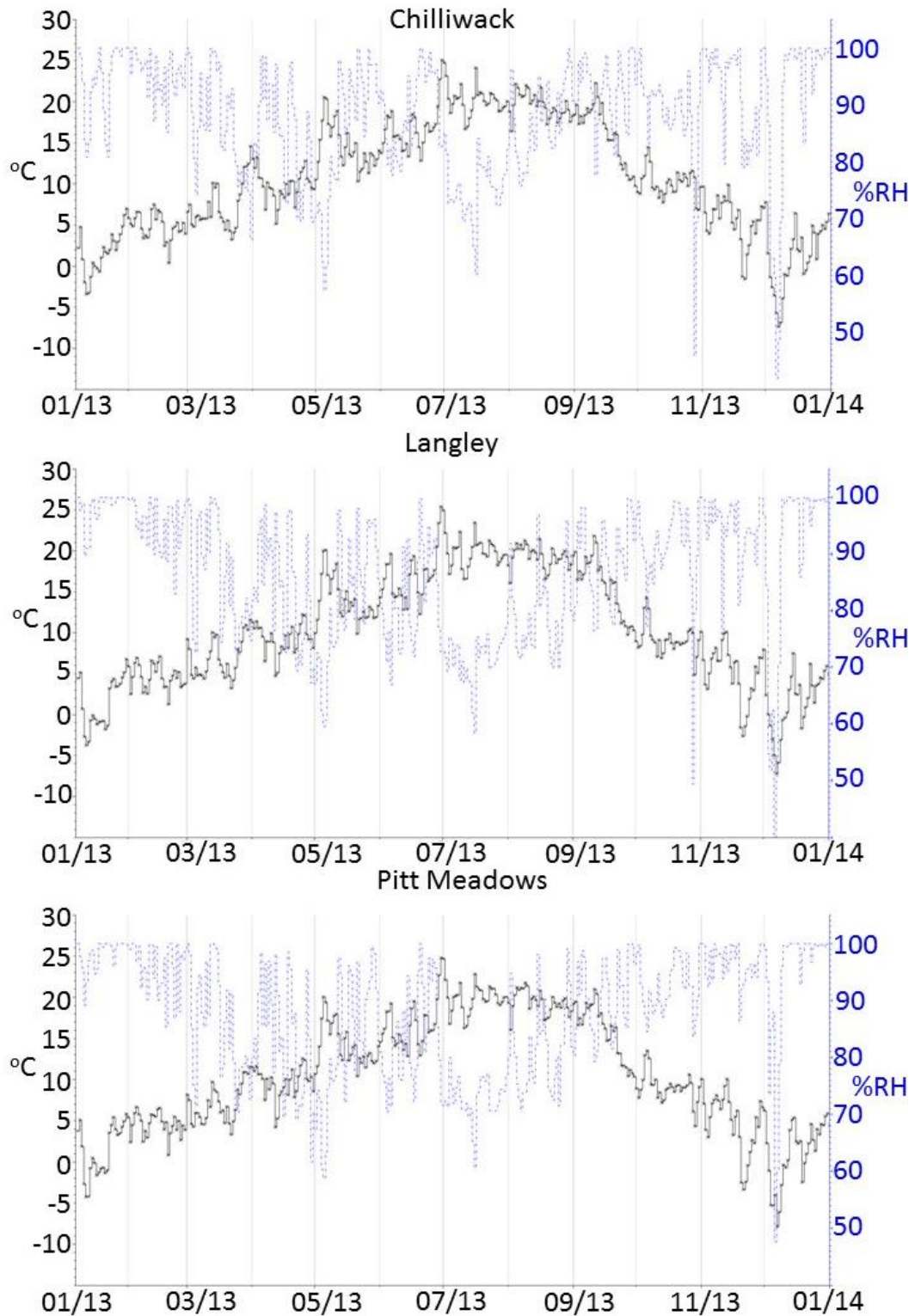
Appendix A.3. Average daily temperature and relative humidity for three trial sites in the Fraser Valley, BC, Canada in 2013 (black line – temperature, blue line – relative humidity).

Appendix A.4. Standard concentrations for three biochemical assays used to compare potential human health benefits in blue honeysuckle with blueberry, raspberry and strawberry in 2012/2013 in the Fraser Valley, BC, Canada (DMSO – dimethyl sulfide, GA – gallic acid, AA – ascorbic acid). (A) Folin Ciocalteau assay for total phenolics (B) Trolox antioxidant capacity assay (C) ferric reducing antioxidant potential assay.

A	Standard	µL 0.25 mM Trolox	µL DMSO	[Trolox] mM	µmol Trolox
	1 (Blank)	0	1000	0	0
	2	100	900	0.025	0.00025
	3	200	800	0.05	0.0005
	4	300	700	0.075	0.00075
	5	400	600	0.1	0.001
	6	600	400	0.15	0.0015
	7	800	200	0.2	0.002
	8	1000	0	0.25	0.0025

B	Standard	µL 1 mM GA	µL Water	[GA] µM	µmol GA
	1 (Blank)	0	1000	0	0
	2	100	900	100	0.01
	3	200	800	200	0.02
	4	300	700	300	0.03
	5	400	600	400	0.04
	6	600	400	600	0.06
	7	800	200	800	0.08
	8	1000	0	1000	0.1

C	Standard	µL 1 mM AA	µL Water	[AA] µM	µmol AA
	1 (Blank)	0	1000	0	0
	2	100	900	100	0.01
	3	200	800	200	0.02
	4	300	700	300	0.03
	5	400	600	400	0.04
	6	600	400	600	0.06
	7	800	200	800	0.08
	8	1000	0	1000	0.1

Appendix A.5. Complete list of chemicals used for biochemical assays related to fruit quality and nutritional content in blue honeysuckle and three comparison crops in 2012/2013 in the Fraser Valley, BC, Canada (IUPAC – International Union of Pure and Applied Chemistry).

Common Name	IUPAC Name	Chemical Formula
Methanol	Methanol	CH_3OH
Formic acid	Formic acid	CH_2O_2
Trolox	6-hydroxy-2,5,7,8-tetramethylchroman-2-carboxylic acid	$C_{14}H_{18}O_4$
DMSO	Dimethyl sulfoxide	C_2H_6OS
ABTS	2,2-Azino-bis(3-ethylbenzthiazoline-6-sulfonic acid)	$C_{18}H_{24}N_6O_6S_4$
Potassium persulfate	Potassium persulfate	$K_2S_2O_8$
diH$_2$0	Deionized water	H_20
sodium bicarbonate	Sodium hydrogen carbonate	$NaHCO_3$
Gallic acid	3,4,5-trihydroxybenzoic acid	$C_7H_6O_5$
Phosphomolybdate	Phosphomolybdic acid	$H_3PMo_{12}O_{40}$
Phosphotungstate	Phosphotungstic acid	$H_3PW_{12}O_{40}$
Sodium acetate	Sodium acetate	$C_2H_3NaO_2$
Acetic acid	Acetic acid	$C_2H_4O_2$
TPTZ	2,4,6-Trispyridyl-s-triazine	$C_{18}H_{12}N_6$
Hydrochloric acid	Hydrochloric acid	HCl
Ferric chloride	Iron (III) chloride	$FeCl_3$
Vitamin C	L-ascorbic acid	$C_6H_8O_6$

Appendix A.6. Heuristics used for comparison of foundation and improved blue honeysuckle groups in 2012/2013 in the Fraser Valley, BC, Canada (A) Correlations (B) Heritability.

A Convention	Correlation Coefficient (r) Range	B Convention	Heritability Estimate
Perfect	1.00 / -1.00	Very high	0.80 to 0.99
Very high	0.90 to 0.99 / -0.90 to -0.99	High	0.70 to 0.79
High	0.70 to 0.89 / -0.70 to -0.89	Moderately high	0.60 to 0.69
Moderate	0.50 to 0.69 / -0.50 to -0.69	Moderate	0.40 to 0.59
Low	0.30 to 0.49 / -0.30 to -0.49	Low	0.20 to 0.39
Little to none	0.00 to 0.29 / 0.00 to -0.29	Negligible	0.00 to 0.19

9.2 Appendix B

Appendix B.1. Foundation Germplasm: Average Julian date +/- SE for bud break in blue honeysuckle and comparison crops in 2012/2013 in the Fraser Valley, BC, Canada (genotypes not connected by the same letter are statistically different, $p < 0.05$, n=18, J – Japanese, K – Kuril, R – Russian).

Genotype	10% Bud Break	50% Bud Break	90% Bud Break
J-21-78	45.5 ± 0.5 h-j	48.9 ± 0.8 f-h	53.6 ± 1.0 h
J-22-14	45.3 ± 0.5 g-j	49.4 ± 0.8 gh	54.4 ± 1.0 h
J-41-83	40.1 ± 0.7 a-e	42.9 ± 0.5 a-d	46.4 ± 0.3 b-e
J-42-45	42.1 ± 0.5 c-h	45.4 ± 0.4 c-e	49.4 ± 0.4 fg
J-43-87	42.0 ± 0.7 c-h	45.8 ± 0.2 d-f	49.3 ± 0.3 fg
J-444-39	43.7 ± 0.6 e-i	46.3 ± 0.5 e-g	50.1 ± 0.7 fg
J-45-14	43.3 ± 0.5 d-h	46.7 ± 0.4 e-g	50.8 ± 0.5 g
J-46-55	47.7 ± 0.6 jk	52.9 ± 1.0 ij	58.4 ± 1.3 i
J-56-18	43.9 ± 0.4 f-i	46.2 ± 0.4 ef	50.2 ± 0.5 g
J-66-53	48.7 ± 0.9 jk	54.1 ± 1.4 j	59.6 ± 1.4 ij
J-73-39	47.2 ± 1.0 i-k	50.3 ± 1.1 hi	54.4 ± 1.1 h
K-3-03	61.7 ± 2.7 n	65.8 ± 2.5 l-n	71.9 ± 1.9 op
K-3-05	62.1 ± 2.7 n	66.4 ± 2.4 mn	73.0 ± 1.6 p
K-3-06	61.7 ± 2.7 n	66.0 ± 2.5 mn	72.3 ± 1.7 p
K-3-07	62.3 ± 2.6 n	65.9 ± 2.4 l-n	71.8 ± 1.8 op
K-97-12	49.8 ± 1.1 k	55.8 ± 1.7 j	61.4 ± 1.8 j
R-2-06	37.5 ± 0.9 ab	40.2 ± 0.5 a	43.9 ± 0.3 ab
R-2-07	39.0 ± 0.5 a-c	41.6 ± 0.3 ab	44.5 ± 0.3 ab
R-2-10	39.8 ± 0.5 a-d	42.8 ± 0.5 a-d	45.9 ± 0.5 b-d
R-2-11	39.4 ± 0.5 a-c	42.5 ± 0.4 a-c	45.2 ± 0.4 a-c
R-2-13	39.0 ± 0.6 a-c	41.4 ± 0.5 ab	45.0 ± 0.3 a-c
R-2-14	36.8 ± 0.0 a	40.5 ± 0.0 a	44.8 ± 0.0 ab
R-2-16	37.2 ± 0.9 a	39.9 ± 0.5 a	43.1 ± 0.3 a
R-27-35	41.9 ± 0.5 c-g	45.1 ± 0.5 c-e	48.2 ± 0.7 d-g

Appendix B.1. Continued. Foundation Germplasm: Average Julian date +/- SE for bud break in blue honeysuckle and comparison crops (genotypes not connected by the same letter are statistically different, p < 0.05, n=18, J – Japanese, K – Kuril, R – Russian).

Genotype	10% Bud Break	50% Bud Break	90% Bud Break
J-PP	40.8 ± 0.5 b-f	43.8 ± 0.3 b-e	47.5 ± 0.3 c-f
'Borealis'	43.0 ± 0.5 d-h	46.4 ± 0.5 e-g	50.0 ± 0.7 fg
'Tundra'	43.8 ± 0.5 f-i	46.5 ± 0.6 e-g	50.4 ± 0.7 g
'Indigo Gem'	41.7 ± 0.5 c-f	45.4 ± 0.7 c-e	48.9 ± 0.8 e-g
Blueberry			
'Bluecrop'	59.1 ± 2.5 mn	63.6 ± 2.7 lm	68.6 ± 2.5 l-n
'Duke'	61.1 ± 2.3 n	65.7 ± 2.2 l-n	69.3 ± 2.1 m-o
'Elliott'	56.8 ± 0.0 lm	62.3 ± 0.0 l	66.1 ± 0.0 kl
'Reka'	57.1 ± 2.1 lm	62.8 ± 2.3 l	67.3 ± 2.3 k-m
Raspberry			
'Cascade Bounty'	62.2 ± 1.2 n	67.2 ± 0.8 n	70.9 ± 0.6 n-p
'Chemainus'	58.8 ± 1.1 mn	63.3 ± 1.0 lm	68.3 ± 0.8 lm
'Meeker'	66.4 ± 2.5 o	73.1 ± 1.7 o	78.4 ± 1.3 q
'Saanich'	54.8 ± 1.3 l	59.2 ± 1.4 k	64.7 ± 1.0 k

Appendix B.2. Foundation Germplasm: Average Julian date +/- SE for flowering onset in blue honeysuckle and comparison crops in 2012/2013 in the Fraser Valley, BC, Canada (genotypes not connected by the same letter are statistically different, $p < 0.05$, n=18, J – Japanese, K – Kuril, R – Russian).

Genotype	First Open Flower	30% Flowering Onset	90% Flowering Onset
J-21-78	89.4 ± 0.7 i-k	92.8 ± 0.8 gh	100.3 ± 1.0 h
J-22-14	94.8 ± 0.8 m	98.2 ± 0.9 l	105.8 ± 0.7 j
J-41-83	88.4 ± 0.7 ij	92.6 ± 0.6 g	99.4 ± 0.7 h
J-42-45	90.6 ± 1.0 i-l	95.2 ± 0.7 ij	104.1 ± 0.7 ij
J-43-87	92.0 ± 0.5 j-m	95.8 ± 0.8 i-k	104.1 ± 0.7 ij
J-444-39	93.5 ± 0.8 lm	96.6 ± 0.7 i-l	101.8 ± 0.4 hi
J-45-14	80.3 ± 1.6 fg	91.1 ± 1.0 fg	100.5 ± 0.8 h
J-46-55	93.1 ± 1.3 k-m	97.4 ± 1.3 j-l	105.3 ± 0.7 j
J-56-18	91.8 ± 0.9 j-m	96.1 ± 0.8 i-l	101.3 ± 0.6 h
J-66-53	92.1 ± 1.0 j-m	97.4 ± 0.7 j-l	104.3 ± 0.8 j
J-73-39	94.8 ± 0.7 m	97.9 ± 0.8 kl	104.8 ± 0.6 j
K-3-03	103.2 ± 0.5 n	107.8 ± 0.5 m	113.2 ± 0.5 k
K-3-05	102.6 ± 0.5 n	107.6 ± 0.5 m	113.2 ± 0.5 k
K-3-06	103.6 ± 0.7 n	108.6 ± 0.5 m	114.1 ± 0.4 k
K-3-07	103.3 ± 0.7 n	108.1 ± 0.6 m	113.8 ± 0.6 k
K-97-12	89.5 ± 1.3 i-k	95.0 ± 1.0 hi	101.0 ± 0.9 h
R-2-06	64.8 ± 3.5 bc	78.4 ± 1.7 b	87.8 ± 0.8 bc
R-2-07	54.0 ± 2.0 a	73.9 ± 0.9 a	83.6 ± 0.5 a
R-2-10	68.6 ± 2.7 cd	79.6 ± 1.4 bc	86.8 ± 0.7 bc
R-2-11	67.4 ± 2.7 b-d	81.2 ± 1.1 c	88.7 ± 0.9 cd
R-2-13	63.8 ± 3.2 b	80.8 ± 1.5 c	88.7 ± 0.8 c
R-2-14	70.9 ± 0.0 de	81.0 ± 0.0 cd	89.3 ± 0.0 c-e
R-2-16	55.3 ± 2.6 a	77.3 ± 1.2 b	85.6 ± 0.5 ab
R-27-35	81.3 ± 0.9 fg	87.7 ± 0.3 e	91.2 ± 0.3 d-f

Appendix B.2. Continued. Foundation Germplasm: Average Julian date +/- SE for flowering onset in blue honeysuckle and comparison crops in 2012/2013 in the Fraser Valley, BC, Canada (genotypes not connected by the same letter are statistically different, $p < 0.05$, n=18, J – Japanese, K – Kuril, R – Russian).

Genotype	First Open Flower	30% Flowering Onset	90% Flowering Onset
J-PP	78.9 ± 2.2 f	89.1 ± 0.8 ef	93.4 ± 0.9 f
'Borealis'	87.5 ± 0.6 hi	91.9 ± 0.7 g	96.9 ± 1.0 g
'Tundra'	84.2 ± 1.2 gh	88.3 ± 1.1 e	92.6 ± 1.2 f
'Indigo Gem'	74.1 ± 2.2 e	83.9 ± 1.1 d	91.2 ± 1.1 ef
Blueberry			
'Bluecrop'	119.3 ± 1.0 p	126.4 ± 1.1 op	131.7 ± 1.2 mn
'Duke'	120.8 ± 1.1 pq	125.6 ± 1.0 o	130.7 ± 1.0 m
'Elliott'	124.7 ± 0.0 qr	130.9 ± 0.0 qr	136.1 ± 0.0 op
'Reka'	112.0 ± 0.9 o	117.5 ± 1.4 n	127.0 ± 1.2 l
Raspberry			
'Cascade Bounty'	139.2 ± 1.0 t	146.1 ± 1.2 s	152.4 ± 1.2 q
'Chemainus'	141.1 ± 1.1 t	149.0 ± 1.5 t	155.3 ± 1.4 rs
'Meeker'	143.1 ± 1.1 t	150.7 ± 1.0 t	157.1 ± 0.7 s
'Saanich'	142.4 ± 1.1 t	149.3 ± 1.0 t	154.3 ± 1.2 qr
Strawberry			
'Puget Reliance'	122.0 ± 1.8 pq	128.8 ± 1.7 q	133.4 ± 1.6 no
'Rainier'	129.0 ± 1.4 s	132.2 ± 1.5 r	136.5 ± 1.6 p
'Stolo'	127.9 ± 1.2 rs	131.7 ± 1.2 r	135.4 ± 1.3 op
'Totem'	123.4 ± 1.4 q	128.6 ± 1.5 pq	133.2 ± 1.7 no

Appendix B.3. Foundation Germplasm: Average Julian date +/- SE for fruit colouring and harvest phenophases in blue honeysuckle and comparison crops in 2012/2013 in the Fraser Valley, BC, Canada (genotypes not connected by the same letter are statistically different, $p < 0.05$, n=18, J – Japanese, K – Kuril, R – Russian).

Genotype	50% Blue	75% Blue	100% Blue	First/Sole Harvest	Final Harvest
J-21-78	149.4 ± 0.9 hi	154.1 ± 1.1 hi	163.2 ± 0.9 jk	166.2 ± 1.0 f-h	-
J-22-14	151.7 ± 1.1 j	156.9 ± 1.0 j	165.4 ± 1.1 l	167.9 ± 1.3 h-j	-
J-41-83	146.9 ± 1.0 g	151.7 ± 0.9 g	161.9 ± 0.8 ij	164.8 ± 1.0 fg	-
J-42-45	149.6 ± 0.9 hi	154.2 ± 1.0 hi	163.1 ± 0.9 jk	165.8 ± 1.1 f-h	-
J-43-87	149.7 ± 0.9 hi	154.3 ± 1.0 hi	162.9 ± 1 i-k	165.8 ± 1.1 f-h	-
J-444-39	155.1 ± 0.9 k	158.9 ± 1.2 k	166.6 ± 1.2 lm	169.6 ± 1.4 j-l	-
J-45-14	145.0 ± 1.0 f	150.6 ± 1.3 g	159.6 ± 1.1 h	162.0 ± 1.2 e	-
J-46-55	152.9 ± 1.2 j	158.5 ± 1.3 k	167.9 ± 1.2 mn	170.6 ± 1.3 kl	-
J-56-18	152.2 ± 0.7 j	157.7 ± 0.7 jk	168.3 ± 0.7 n	171.1 ± 0.9 lm	-
J-66-53	149.8 ± 0.9 i	155.2 ± 1.1 hi	163.5 ± 1.0 k	165.6 ± 1.1 fg	-
J-73-39	149.9 ± 0.9 i	155.4 ± 0.9 i	165.5 ± 1.2 l	168.8 ± 1.3 i-k	-
K-3-03	160.5 ± 0.8 l	163.9 ± 0.9 l	170.3 ± 0.9 o	173.2 ± 1.0 mn	-
K-3-05	160.3 ± 0.8 l	164.3 ± 1.0 l	170.9 ± 0.8 o	173.4 ± 1.0 n	-
K-3-06	159.8 ± 1.0 l	164.1 ± 0.8 l	170.6 ± 0.6 o	173.3 ± 0.6 n	-
K-3-07	160.0 ± 0.8 l	163.4 ± 0.9 l	170.6 ± 0.9 o	174.2 ± 0.8 n	-
K-97-12	147.6 ± 0.0 gh	153.1 ± 0.0 h	161.1 ± 0.0 i	163.5 ± 0.0 ef	-
R-2-06	137.0 ± 0.0 ab	140.9 ± 0.0 ab	144.8 ± 0.0 a	146.5 ± 0.0 ab	-
R-2-07	138.2 ± 1.3 a-c	141.7 ± 1.4 ab	145.3 ± 1.3 a	147.4 ± 1.3 ab	-
R-2-10	137.1 ± 0.0 a-c	140.7 ± 0.0 ab	144.4 ± 0.0 a	146.6 ± 0.0 ab	-
R-2-11	138.8 ± 0.0 b-d	142.6 ± 0.0 b-d	147.0 ± 0.0 bc	149.0 ± 0.0 b	-
R-2-13	136.6 ± 0.0 b-d	139.8 ± 0.0 a-c	143.7 ± 0.0 ab	146.5 ± 0.0 ab	-
R-2-14	140.5 ± 0.0 de	145.0 ± 0.0 de	149.4 ± 0.0 cd	152.1 ± 0.0 c	-
R-2-16	136.5 ± 0.0 a	140.7 ± 0.0 a	144.6 ± 0.0 a	146.3 ± 0.0 a	-
R-27-35	141.3 ± 1.0 e	144.5 ± 1.1 e	150.4 ± 0.7 d-f	152.1 ± 0.8 c	-

Appendix B.3. Continued. Foundation Germplasm: Average Julian date +/- SE for fruit colouring and harvest phenophases in blue honeysuckle and comparison crops in 2012/2013 in the Fraser Valley, BC, Canada (genotypes not connected by the same letter are statistically different, $p < 0.05$, n=18, J – Japanese, K – Kuril, R – Russian).

Genotype	50% Blue	75% Blue	100% Blue	First/Sole Harvest	Final Harvest
J-PP	142.3 ± 1.1 e	145.0 ± 1.1 e	151.1 ± 1.0 ef	153.3 ± 1.0 c	-
'Borealis'	143.4 ± 0.0 f	147.4 ± 0.0 f	153.3 ± 0.0 g	156.8 ± 0.5 d	-
'Tundra'	138.4 ± 0.0 b-d	143.0 ± 0.0 c-e	149.8 ± 0.0 de	152.1 ± 0.0 c	-
'Indigo Gem'	138.9 ± 0.0 cd	143.7 ± 0.0 de	151.5 ± 0.0 f	153.8 ± 0.0 c	-
Blueberry					
'Bluecrop'	-	-	-	199.7 ± 1.9 q	212.7 ± 2.2 c
'Duke'	-	-	-	189.2 ± 0.9 p	201.5 ± 1.3 b
'Elliott'	-	-	-	223.7 ± 1.6 r	240.0 ± 3.2 d
'Reka'	-	-	-	188.2 ± 0.8 p	200.0 ± 2.3 b
Raspberry					
'Cascade Bounty'	-	-	-	184.9 ± 1.9 o	213.1 ± 1.7 c
'Chemainus'	-	-	-	183.4 ± 2.1 o	211.8 ± 2.3 c
'Meeker'	-	-	-	184.4 ± 1.2 o	210.2 ± 1.2 c
'Saanich'	-	-	-	185.5 ± 1.8 o	212.1 ± 1.7 c
Strawberry					
'Puget Reliance'	-	-	-	166.7 ± 1.7 g-i	183.5 ± 1.7 a
'Rainier'	-	-	-	170.9 ± 1.8 kl	185.9 ± 2.0 a
'Stolo'	-	-	-	170.2 ± 1.6 kl	183.6 ± 1.8 a
'Totem'	-	-	-	166.8 ± 1.5 g-i	184.9 ± 1.5 a

Appendix B.4. Average daily temperatures for three locations for the early, mid and late thirds of each month in 2012/2013 (C – Chilliwack, L – Langley, PM – Pitt Meadows).

	Year	Site	January			February			March			April		
			Early	Mid	Late	Early	Mid	Late	Early	Mid	Late	Early	Mid	Late
Average Temperature (°C)	2012	C	4.6	-4.2	2.5	5.0	5.2	3.4	4.5	3.6	6.7	8.6	9.7	12.0
		L	5.4	-3.4	4.1	4.9	4.7	3.5	4.3	-3.0	6.4	7.9	9.0	11.6
		PM	5.1	-3.3	3.8	4.2	5.1	3.0	4.4	-3.0	6.6	8.3	9.4	12.1
	2013	C	1.8	-0.7	3.5	5.0	4.9	4.4	5.9	7.1	8.6	10.5	8.6	10.3
		L	2.0	-1.5	3.2	4.6	4.8	4.3	5.6	7.2	7.8	9.8	8.1	9.7
		PM	2.5	-1.6	3.3	4.5	4.9	4.2	5.6	7.2	8.2	10.2	8.4	10.2
	2012/2013	C	3.2	-2.5	3.0	5.0	5.0	3.9	5.2	5.4	7.7	9.6	9.2	11.2
		L	3.7	-2.5	3.7	4.7	4.8	3.9	5.0	2.1	7.1	8.9	8.5	10.7
		PM	3.8	-2.5	3.6	4.3	5.0	3.6	5.0	2.1	7.4	9.3	8.9	11.2
	Average		3.6	-2.5	3.4	4.7	4.9	3.8	5.1	3.2	7.4	9.2	8.9	11.0

	Year	Site	May			June			July			August		
			Early	Mid	Late	Early	Mid	Late	Early	Mid	Late	Early	Mid	Late
Average Temperature (°C)	2012	C	11.4	15.5	13.9	12.1	14.7	16.4	18.1	20.2	18.2	21.3	21.9	17.4
		L	10.4	14.1	14.0	12.1	14.4	15.9	17.6	19.9	17.9	20.3	20.8	16.2
		PM	10.6	14.3	13.8	12.3	14.3	16.1	17.9	20.5	18.0	20.7	21.5	16.8
	2013	C	16.5	14.7	12.5	16.3	15.4	18.4	21.0	19.8	19.8	20.4	19.6	18.6
		L	15.9	14.1	12.1	16.2	15.4	18.7	20.3	19.6	19.7	19.8	19.0	19.0
		PM	16.0	14.3	12.4	16.1	15.5	18.2	20.3	19.5	20.0	20.2	19.0	19.0
	2012/2013	C	14.0	15.1	13.2	14.2	15.1	17.4	19.5	20.0	19.0	20.9	20.7	18.0
		L	13.1	14.1	13.0	14.1	14.9	17.3	18.9	19.8	18.8	20.0	19.9	17.6
		PM	13.3	14.3	13.1	14.2	14.9	17.1	19.1	20.0	19.0	20.4	20.2	17.9
	Average		13.5	14.5	13.1	14.2	14.9	17.3	19.2	19.9	18.9	20.5	20.3	17.8

Appendix B.4. Continued. Average daily temperatures for three locations for the early, mid and late thirds of each month in 2012/2013 (C – Chilliwack, L – Langley, PM – Pitt Meadows).

	Year	Site	September			October			November			December		
			Early	Mid	Late	Early	Mid	Late	Early	Mid	Late	Early	Mid	Late
Average Temperature (°C)	2012	C	17.3	15.9	14.6	11.5	11.2	7.6	7.7	5.2	4.8	4.7	2.1	0.5
		L	16.3	15.4	14.1	10.6	10.9	7.8	7.5	5.7	4.6	4.7	2.6	1.8
		PM	16.7	15.6	14.4	10.7	10.9	8.2	7.6	6.1	5.0	4.6	2.8	2.6
	2013	C	18.6	17.7	11.9	10.9	9.4	10.0	6.6	5.8	4.2	*-2.3*	1.6	3.7
		L	18.3	17.2	11.7	10.3	8.4	8.7	6.4	6.1	2.9	*-1.6*	2.2	3.8
		PM	18.4	17.2	12.0	10.3	8.5	8.4	6.6	5.5	2.3	*-2.4*	1.8	3.6
	2012/ 2013	C	18.0	16.8	13.2	11.2	10.3	8.8	7.1	5.5	4.5	1.2	1.9	2.1
		L	17.3	16.3	12.9	10.4	9.7	8.2	7.0	5.9	3.7	1.6	2.4	2.8
		PM	17.5	16.4	13.2	10.5	9.7	8.3	7.1	5.8	3.7	1.1	2.3	3.1
	Average		17.6	16.5	13.1	10.7	9.9	8.4	7.1	5.7	4.0	1.3	2.2	2.7

Appendix B.5. Daily maximum temperatures for three locations for the early, mid and late thirds of each month in 2012/2013 (C – Chilliwack, L – Langley, PM – Pitt Meadows).

Year	Site	January			February			March			April		
		Early	Mid	Late	Early	Mid	Late	Early	Mid	Late	Early	Mid	Late
Maximum Temperature (°C)													
2012	C	8.5	*-1.0*	5.6	10.2	9.0	7.2	8.3	8.3	12.8	17.1	17.2	18.5
	L	9.6	1.7	7.4	11.5	8.0	7.7	7.9	2.4	12.2	15.5	15.6	17.1
	PM	8.7	2.9	6.9	11.8	8.9	8.3	8.9	3.3	12.9	17.0	17.1	18.6
2013	C	5.0	4.0	6.2	10.1	9.6	8.5	11.7	12.1	19.1	16.8	15.6	18.8
	L	5.4	3.2	5.5	8.5	8.7	7.7	10.8	11.3	16.7	14.4	13.6	16.6
	PM	6.0	4.3	5.6	9.1	9.8	7.8	11.9	12.3	18.9	15.8	15.8	18.5
2012/2013	C	6.7	1.5	5.9	10.2	9.3	7.9	10.0	10.2	15.9	17.0	16.4	18.7
	L	7.5	2.4	6.4	10.0	8.4	7.7	9.3	6.8	14.5	14.9	14.6	16.8
	PM	7.4	3.6	6.3	10.5	9.4	8.0	10.4	7.8	15.9	16.4	16.4	18.6
Average		7.2	2.5	6.2	10.2	9.0	7.9	9.9	8.3	15.4	16.1	15.8	18.0

Year	Site	May			June			July			August		
		Early	Mid	Late	Early	Mid	Late	Early	Mid	Late	Early	Mid	Late
Maximum Temperature (°C)													
2012	C	20.3	27.1	19.7	15.7	18.9	22.7	25.2	26.3	24.1	31.3	33.0	27.2
	L	16.7	23.2	20.3	17.0	19.7	22.3	25.0	26.8	25.0	29.2	30.6	24.7
	PM	18.3	25.4	21.1	17.3	20.3	23.5	26.4	28.8	25.5	30.1	32.6	25.5
2013	C	28.4	20.5	17.1	23.1	19.8	24.1	29.7	28.5	29.8	30.2	27.2	25.2
	L	25.9	20.0	16.9	23.5	21.1	24.4	28.6	28.3	28.4	28.0	25.9	26.5
	PM	26.9	20.3	17.1	23.1	20.7	23.1	27.7	27.3	28.7	28.0	25.6	26.1
2012/2013	C	24.4	23.8	18.4	19.4	19.4	23.4	27.4	27.4	27.0	30.7	30.1	26.2
	L	21.3	21.6	18.6	20.2	20.4	23.4	26.8	27.5	26.7	28.6	28.2	25.6
	PM	22.6	22.8	19.1	20.2	20.5	23.3	27.1	28.1	27.1	29.1	29.1	25.8
Average		22.7	22.7	18.7	19.9	20.1	23.3	27.1	27.7	26.9	29.5	29.1	25.9

Appendix B.5. Continued. Daily maximum temperatures for three locations for the early, mid and late thirds of each month in 2012/2013 (C – Chilliwack, L – Langley, PM – Pitt Meadows).

	Year	Site	September			October			November			December		
			Early	Mid	Late	Early	Mid	Late	Early	Mid	Late	Early	Mid	Late
Maximum Temp-erature (°C)	2012	C	28.9	29.8	22.9	21.9	14.9	11.5	11.8	8.1	7.8	7.0	4.2	2.5
		L	26.3	27.0	21.2	20.6	14.0	11.4	12.2	9.0	8.4	7.2	5.0	3.9
		PM	27.9	29.3	22.4	22.8	14.1	11.6	13.0	9.4	8.4	7.3	4.9	5.0
	2013	C	24.6	25.3	16.6	18.2	20.5	18.0	10.5	9.2	9.4	1.4	4.6	7.0
		L	24.9	25.0	16.2	16.7	15.7	15.1	9.7	9.7	8.9	1.9	4.8	6.9
		PM	25.1	25.0	16.5	16.8	17.1	16.8	10.5	10.7	9.9	4.0	4.8	6.8
	2012/ 2013	C	26.7	27.6	19.7	20.0	17.7	14.8	11.2	8.7	8.6	4.2	4.4	4.8
		L	25.6	26.0	18.7	18.6	14.9	13.2	11.0	9.3	8.7	4.5	4.9	5.4
		PM	26.5	27.1	19.4	19.8	15.6	14.2	11.8	10.1	9.2	5.7	4.9	5.9
	Average		26.3	26.9	19.3	19.5	16.1	14.1	11.3	9.4	8.8	4.8	4.7	5.3

Appendix B.6. Daily minimum temperatures for three locations for the early, mid and late thirds of each month in 2012/2013 (C – Chilliwack, L – Langley, PM – Pitt Meadows).

	Year	Site	January			February			March			April		
			Early	Mid	Late	Early	Mid	Late	Early	Mid	Late	Early	Mid	Late
Minimum Temperature (°C)	2012	C	1.8	-7.2	-0.1	0.7	2.1	0.5	1.4	0.2	1.5	1.7	4.3	7.2
		L	2.7	-7.7	1.0	0.5	1.4	0.4	0.7	-7.2	1.3	0.6	3.9	7.0
		PM	2.6	-9.2	0.9	-0.4	2.1	-1.6	0.7	-9.0	1.6	0.6	3.5	7.1
	2013	C	-0.7	-4.1	1.5	1.1	1.0	1.7	1.1	3.6	0.6	6.5	3.3	2.9
		L	-0.7	-4.7	1.2	0.9	1.1	1.0	0.8	4.1	0.3	5.9	3.5	2.4
		PM	0.2	-5.4	1.5	0.5	1.1	1.0	0.2	3.5	-0.2	6.1	2.6	2.3
	2012/ 2013	C	0.6	-5.7	0.7	0.9	1.5	1.1	1.3	1.9	1.1	4.1	3.8	5.0
		L	1.0	-6.2	1.1	0.7	1.2	0.7	0.8	-1.6	0.8	3.3	3.7	4.7
		PM	1.4	-7.3	1.2	0.1	1.6	-0.3	0.4	-2.8	0.7	3.3	3.0	4.7
	Average		1.0	-6.4	1.0	0.6	1.5	0.5	0.8	-0.8	0.9	3.6	3.5	4.8

	Year	Site	May			June			July			August		
			Early	Mid	Late	Early	Mid	Late	Early	Mid	Late	Early	Mid	Late
Minimum Temperature (°C)	2012	C	4.5	5.4	8.9	9.1	9.6	11.3	11.0	14.6	12.9	13.1	12.3	9.4
		L	4.7	4.2	8.6	7.9	8.2	10.2	10.0	13.6	11.5	12.0	11.7	8.4
		PM	4.1	3.4	8.3	8.2	8.6	10.6	10.5	14.3	12.2	13.0	12.2	9.5
	2013	C	5.8	10.1	8.5	9.1	10.8	13.1	12.2	10.9	9.9	13.1	14.1	13.0
		L	5.2	8.9	7.7	7.9	9.5	12.9	11.3	9.7	10.0	12.0	12.6	12.1
		PM	5.3	9.2	8.4	8.9	9.9	13.8	12.4	10.8	10.9	12.8	13.1	12.5
	2012/ 2013	C	5.2	7.8	8.7	9.1	10.2	12.2	11.6	12.7	11.4	13.1	13.2	11.2
		L	4.9	6.6	8.1	7.9	8.8	11.6	10.7	11.6	10.7	12.0	12.2	10.3
		PM	4.7	6.3	8.3	8.5	9.3	12.2	11.5	12.6	11.6	12.9	12.7	11.0
	Average		4.9	6.9	8.4	8.5	9.4	12.0	11.2	12.3	11.2	12.7	12.7	10.8

Appendix B.6. Continued. Daily minimum temperatures for three locations for the early, mid and late thirds of each month in 2012/2013 (C – Chilliwack, L – Langley, PM – Pitt Meadows).

	Year	Site	September			October			November			December		
			Early	Mid	Late	Early	Mid	Late	Early	Mid	Late	Early	Mid	Late
Minimum Temp-erature (°C)	2012	C	7.8	5.2	7.3	3.3	8.3	4.7	4.1	2.3	2.2	3.2	0.5	*-1.6*
		L	7.4	5.7	7.3	2.0	8.0	4.6	4.2	2.6	1.2	2.6	0.7	0.0
		PM	7.9	5.9	7.7	2.4	8.0	5.5	3.9	3.5	1.6	1.7	1.0	0.7
	2013	C	13.8	12.2	8.2	5.7	1.8	4.1	3.3	2.5	0.6	*-5.2*	*-1.1*	0.8
		L	12.3	11.4	8.2	4.7	3.0	3.6	3.5	2.6	*-1.2*	*-4.8*	*-1.0*	1.0
		PM	12.5	11.6	8.5	4.8	3.5	3.6	3.1	1.1	*-2.0*	*-7.4*	*-1.9*	0.0
	2012/ 2013	C	10.8	8.7	7.8	4.5	5.1	4.4	3.7	2.4	1.4	*-1.0*	*-0.3*	*-0.4*
		L	9.9	8.5	7.8	3.3	5.5	4.1	3.9	2.6	*-0.0*	*-1.1*	*-0.1*	0.5
		PM	10.2	8.8	8.1	3.6	5.8	4.5	3.5	2.3	*-0.2*	*-2.8*	*-0.5*	0.3
	Average		10.3	8.7	7.9	3.8	5.4	4.3	3.7	2.4	0.4	*-1.6*	*-0.3*	0.2

Appendix B.7. Average relative humidity for three locations for the early, mid and late thirds of each month in 2012/2013 (C – Chilliwack, L – Langley, PM – Pitt Meadows, RH – relative humidity).

Year	Site	January			February			March			April		
		Early	Mid	Late	Early	Mid	Late	Early	Mid	Late	Early	Mid	Late
2012	C	92.3	90.6	93.8	83.2	95.6	84.9	92.9	94.7	84.9	78.4	86.5	86.5
	L	88.0	90.1	91.8	87.2	95.6	81.9	91.2	88.1	82.3	76.2	84.7	84.4
	PM	95.0	93.3	95.6	92.6	95.3	86.1	91.4	92.5	82.8	76.5	84.0	83.4
2013	C	94.1	90.9	96.0	97.2	93.4	95.5	89.1	91.9	79.0	89.3	86.5	76.6
	L	99.3	96.2	99.7	96.4	94.3	94.7	90.0	91.2	78.6	89.2	86.5	76.3
	PM	99.1	96.6	99.5	96.8	95.1	95.5	88.6	91.1	78.2	88.5	85.4	76.1
2012/ 2013	C	93.2	90.7	94.9	90.2	94.5	90.2	91.0	93.3	82.0	83.9	86.5	81.5
	L	93.7	93.2	95.8	91.8	94.9	88.3	90.6	89.6	80.5	82.7	85.6	80.3
	PM	97.0	95.0	97.5	94.7	95.2	90.8	90.0	91.8	80.5	82.5	84.7	79.7
Average		94.6	92.9	96.1	92.2	94.9	89.8	90.5	91.6	81.0	83.0	85.6	80.5

Row label for the data rows above: Average RH (%)

Year	Site	May			June			July			August		
		Early	Mid	Late	Early	Mid	Late	Early	Mid	Late	Early	Mid	Late
2012	C	75.6	62.4	83.9	93.4	89.9	86.9	81.4	83.7	85.6	76.5	72.6	75.7
	L	76.0	65.0	76.8	86.3	82.6	82.7	76.6	80.0	79.8	76.6	74.0	77.2
	PM	78.7	67.2	81.4	88.0	87.0	83.1	77.7	78.0	82.3	77.1	72.7	76.4
2013	C	70.6	90.1	94.5	82.9	90.3	92.9	75.3	73.1	76.5	82.4	88.5	90.8
	L	69.2	84.7	90.3	76.6	82.7	86.1	72.0	68.7	73.0	77.6	81.3	79.1
	PM	70.3	86.0	89.8	78.0	84.0	87.8	73.7	71.0	73.3	78.1	83.3	82.0
2012/ 2013	C	73.1	76.3	89.2	88.2	90.1	89.9	78.3	78.4	81.1	79.4	80.5	83.3
	L	72.6	74.8	83.6	81.5	82.6	84.4	74.3	74.3	76.4	77.1	77.7	78.1
	PM	74.5	76.6	85.6	83.0	85.5	85.4	75.7	74.5	77.8	77.6	78.0	79.2
Average		73.4	75.9	86.1	84.2	86.1	86.6	76.1	75.7	78.4	78.0	78.7	80.2

Row label for the data rows above: Average RH (%)

Appendix B.7. Continued. Average relative humidity for three locations for the early, mid and late thirds of each month in 2012/2013 (C – Chilliwack, L – Langley, PM – Pitt Meadows, RH – relative humidity).

	Year	Site	September			October			November			December		
			Early	Mid	Late	Early	Mid	Late	Early	Mid	Late	Early	Mid	Late
Average RH (%)	2012	C	74.1	75.9	86.0	75.5	95.5	94.2	91.1	97.6	95.5	98.1	99.3	94.5
		L	75.0	75.6	84.3	78.2	94.4	94.3	92.0	97.1	97.5	97.8	99.5	98.9
		PM	75.1	75.6	85.3	80.0	94.4	94.3	93.4	97.5	97.8	98.3	99.6	99.1
	2013	C	94.2	89.2	94.4	92.5	89.0	83.6	97.2	93.5	87.3	72.0	96.5	98.4
		L	88.6	85.3	92.1	89.8	93.2	88.5	97.3	91.7	94.1	70.1	97.1	99.0
		PM	89.9	88.1	93.9	91.1	93.0	93.1	97.2	96.0	96.3	82.1	99.0	99.5
	2012/ 2013	C	84.2	82.5	90.2	84.0	92.3	88.9	94.2	95.6	91.4	85.0	97.9	96.5
		L	81.8	80.4	88.2	84.0	93.8	91.4	94.7	94.4	95.8	84.0	98.3	99.0
		PM	82.5	81.8	89.6	85.6	93.7	93.7	95.3	96.8	97.0	90.2	99.3	99.3
	Average		82.8	81.6	89.4	84.5	93.3	91.3	94.7	95.6	94.8	86.4	98.5	98.2

Appendix B.8. Foundation Germplasm: Average Julian date +/- SE for growth cessation and leaf drop phenophases in blue honeysuckle and comparison crops in 2012/2013 in the Fraser Valley, BC, Canada (genotypes not connected by the same letter are statistically different, $p < 0.05$, n=18, J – Japanese, K – Kuril, R – Russian).

Genotype	Growth Cessation	50% Leaf Drop	95% Leaf Drop
J-21-78	150.4 ± 0.8 d	289.0 ± 1.3 j-n	305.2 ± 1.0 i-k
J-22-14	150.2 ± 1.3 d	289.4 ± 1.7 k-n	306.7 ± 1.1 k
J-41-83	156.5 ± 1.1 i	291.7 ± 1.1 n	303.6 ± 0.9 h-j
J-42-45	155.3 ± 0.5 g-i	284.0 ± 1.1 g-i	300.8 ± 0.9 gh
J-43-87	155.1 ± 1.0 g-i	281.8 ± 1.2 gh	300.5 ± 0.9 g
J-444-39	153.1 ± 0.7 e-g	272.4 ± 1.2 de	303.4 ± 1.1 g-j
J-45-14	153.1 ± 0.6 e-g	292.2 ± 1.7 n	306.2 ± 1.1 jk
J-46-55	153.9 ± 0.7 gh	284.2 ± 1.3 g-j	303.6 ± 1.1 h-j
J-56-18	153.4 ± 1.2 fg	284.9 ± 1.2 g-k	305.4 ± 0.7 i-k
J-66-53	155.0 ± 0.6 g-i	290.1 ± 1.4 l-n	306.7 ± 1.0 k
J-73-39	150.7 ± 0.8 d	280.9 ± 2.3 fg	304.4 ± 1.2 i-k
K-3-03	156.0 ± 0.5 hi	285.8 ± 1.5 h-l	303.4 ± 0.6 g-j
K-3-05	156.0 ± 0.5 hi	286.6 ± 1.4 h-m	303.7 ± 0.7 h-j
K-3-06	156.6 ± 0.5 i	288.7 ± 0.7 i-n	304.1 ± 0.6 i-k
K-3-07	155.8 ± 0.6 hi	286.7 ± 0.7 h-m	303.4 ± 0.3 g-j
K-97-12	154.8 ± 0 g-i	289.2 ± 1.4 k-n	302.9 ± 0.8 g-i
R-2-06	145.0 ± 0.8 c	265.2 ± 3.1 bc	286.2 ± 1.9 bc
R-2-07	144.6 ± 1.0 c	272.9 ± 1.3 de	290.5 ± 0.6 de
R-2-10	144.1 ± 0.0 bc	263.5 ± 1.9 b	286.6 ± 0.8 bc
R-2-11	142.1 ± 0.6 ab	257.1 ± 2.1 a	282.7 ± 1.3 a
R-2-13	141.6 ± 0.0 a	254.6 ± 2.0 a	282.7 ± 1.6 a
R-2-14	142.9 ± 0.0 a-c	269.4 ± 0.0 cd	288.5 ± 0.0 cd
R-2-16	141.0 ± 0.9 a	257.4 ± 2.2 a	284.9 ± 1.3 ab
R-27-35	151.1 ± 0.9 de	280.7 ± 1.5 fg	295.4 ± 0.7 f

Appendix B.8. Continued. Foundation Germplasm: Average Julian date +/- SE for growth cessation and leaf drop phenophases in blue honeysuckle and comparison crops in 2012/2013 in the Fraser Valley, BC, Canada (genotypes not connected by the same letter are statistically different, $p < 0.05$, n=18, J – Japanese, K – Kuril, R – Russian).

Genotype	Growth Cessation	50% Leaf Drop	95% Leaf Drop
J-PP	149.1 ± 1.2 d	266.8 ± 2.0 bc	287.6 ± 1.5 bc
'Borealis'	154.5 ± 0.0 g-i	276.7 ± 1.8 ef	293.0 ± 0.9 ef
'Tundra'	153.1 ± 0.0 e-g	272.7 ± 1.5 de	293.1 ± 0.8 ef
'Indigo Gem'	151.3 ± 0.0 d-f	274.3 ± 1.5 de	292.6 ± 1.0 ef
Blueberry			
'Bluecrop'	-	305.6 ± 1.7 pq	317.4 ± 1.3 m
'Duke'	-	290.9 ± 2.8 mn	310.3 ± 1.1 l
'Elliott'	-	311.8 ± 1.3 r	321.5 ± 1.6 n
'Reka'	-	301.3 ± 2.1 op	311.6 ± 1.1 l
Raspberry			
'Cascade Bounty'	-	307.5 ± 1.6 qr	325.1 ± 0.9 o
'Chemainus'	-	306.2 ± 2.6 q	334.2 ± 1.0 p
'Meeker'	-	300.1 ± 3.2 o	327.1 ± 2.8 o
'Saanich'	-	311.6 ± 3.2 r	341.0 ± 0.6 q

Appendix B.9. Foundation Germplasm: Comparisons of parent genotypes used in each hybrid cross combination to generate improved seedling families for phenological traits in 2012/2013 in Chilliwack, BC, Canada (based on linear contrasts extracted from linear mixed model regression, $p < 0.05$, n=6).

		Kuril vs. Japanese	Japanese vs. Russian	Russian vs. Kuril			Kuril vs. Japanese	Japanese vs. Russian	Russian vs. Kuril
10% Bud Break	Earlier	0	16	16	50% Blue	Earlier	1	16	16
	Equal	0	0	0		Equal	1	0	0
	Later	8	0	0		Later	6	0	0
50% Bud Break	Earlier	0	16	16	75% Blue	Earlier	1	16	16
	Equal	0	0	0		Equal	1	0	0
	Later	8	0	0		Later	6	0	0
90% Bud Break	Earlier	0	16	16	100% Blue	Earlier	2	16	16
	Equal	0	0	0		Equal	0	0	0
	Later	8	0	0		Later	6	0	0
First Open Flower	Earlier	1	16	16	Fruit Harvest	Earlier	2	16	16
	Equal	1	0	0		Equal	0	0	0
	Later	6	0	0		Later	6	0	0
30% Flowering Onset	Earlier	1	16	16	Growth Cessation	Earlier	0	15	16
	Equal	1	0	0		Equal	7	1	0
	Later	6	0	0		Later	1	0	0
90% Flowering Onset	Earlier	2	16	16	50% Leaf Drop	Earlier	2	16	16
	Equal	0	0	0		Equal	1	0	0
	Later	6	0	0		Later	5	0	0
					95% Leaf Drop	Earlier	1	16	16
						Equal	3	0	0
						Later	4	0	0

Appendix B.10. Improved Germplasm: Statistical classification (%) of blue honeysuckle hybrids compared with their parent foundation genotypes for spring phenophases in 2012/2013 in Chilliwack, BC, Canada (n=6[1]).

| | | Early | | | Late | | Total | | Early | | | Late | | Total |
		Transgressive Segregants	Parent Types	Intermediates	Parent Types	Transgressive Segregants	Transgressive Segregants		Transgressive Segregants	Parent Types	Intermediates	Parent Types	Transgressive Segregants	Transgressive Segregants
All Improved	10% Bud Break	1.9	29.4	55.6	10.6	2.5	4.4	First Open Flower	2.5	18.8	65.6	13.1	0.0	2.5
Japanese/Kuril		9.4	62.5	21.9	6.3	0.0	9.4		9.4	34.4	56.3	0.0	0.0	9.4
Japanese/Russian		0.0	17.2	53.1	23.4	6.3	6.3		0.0	18.8	50.0	31.3	0.0	0.0
Kuril/Russian		0.0	25.0	75.0	0.0	0.0	0.0		1.6	10.9	85.9	1.6	0.0	1.6
All Improved	50% Bud Break	2.5	20.6	67.5	6.9	2.5	5.0	30% Flowering Onset	3.8	16.9	66.9	6.9	5.6	9.4
Japanese/Kuril		12.5	53.1	31.3	3.1	0.0	12.5		18.8	25.0	56.3	0.0	0.0	18.8
Japanese/Russian		0.0	10.9	67.2	15.6	6.3	6.3		0.0	15.6	53.1	17.2	14.1	14.1
Kuril/Russian		0.0	14.1	85.9	0.0	0.0	0.0		0.0	14.1	85.9	0.0	0.0	0.0
All Improved	90% Bud Break	3.1	20.0	65.6	8.8	2.5	5.6	90% Flowering Onset	3.8	24.4	59.4	6.3	6.3	10.0
Japanese/Kuril		15.6	40.6	43.8	0.0	0.0	15.6		9.4	37.5	50.0	3.1	0.0	9.4
Japanese/Russian		0.0	14.1	57.8	21.9	6.3	6.3		3.1	26.6	40.6	14.1	15.6	18.8
Kuril/Russian		0.0	15.6	84.4	0.0	0.0	0.0		1.6	15.6	82.8	0.0	0.0	1.6

[1]Comparisons made by pairwise comparison using linear contrasts extracted from mixed regression models (p<0.05).

Appendix B.10. Continued. Improved Germplasm: Statistical classification (%) of blue honeysuckle hybrids compared with their parent foundation genotypes for spring phenophases in 2012/2013 in Chilliwack, BC, Canada (n=6[1]).

		Early			Late		Total		Early			Late		Total
		Transgressive Segregants	Parent Types	Intermediates	Parent Types	Transgressive Segregants	Transgressive Segregants		Transgressive Segregants	Parent Types	Intermediates	Parent Types	Transgressive Segregants	Transgressive Segregants
All Improved		9.4	35.6	46.9	6.3	1.9	11.3		7.5	8.8	71.9	7.5	4.4	11.9
Japanese/Kuril	50%	21.9	28.1	34.4	6.3	9.4	31.3	100%	34.4	28.1	25.0	6.3	6.3	40.6
Japanese/Russian	Blue Fruit	0.0	9.4	68.8	9.4	12.5	12.5	Blue Fruit	0.0	0.0	76.6	15.6	7.8	7.8
Kuril/Russian		3.1	6.3	90.6	0.0	0.0	3.1		1.6	7.8	90.6	0.0	0.0	1.6
All Improved		6.3	9.4	71.9	5.6	6.9	13.1		7.5	9.4	71.9	6.9	4.4	11.9
Japanese/Kuril	75%	25.0	25.0	31.3	9.4	9.4	34.4	Fruit	31.3	34.4	25.0	3.1	6.3	37.5
Japanese/Russian	Blue Fruit	0.0	4.7	73.4	9.4	12.5	12.5	Harvest	0.0	0.0	76.6	15.6	7.8	7.8
Kuril/Russian		3.1	6.3	90.6	0.0	0.0	3.1		3.1	6.3	90.6	0.0	0.0	3.1

[1]Comparisons made by pairwise comparison using linear contrasts extracted from mixed regression models (p<0.05).

Appendix B.11. Improved Germplasm: Statistical classification (%) of blue honeysuckle hybrids compared with their parent foundation genotypes for vegetative growth cessation and leaf drop in 2012/2013 in Chilliwack, BC, Canada (n=6[1]).

| | | Early | | | Late | | Total |
		Transgressive Segregants	Parent Types	Intermediates	Parent Types	Transgressive Segregants	Transgressive Segregants
All Improve	Growth Cessation	11.9	9.4	49.4	27.5	1.9	13.8
Japanese/Kuril		56.3	9.4	34.4	0.0	0.0	56.3
Japanese/Russian		1.6	6.3	31.3	56.3	4.7	6.3
Kuril/Russian		0.0	12.5	75.0	12.5	0.0	0.0
All Improve	50% Leaf Drop	1.9	8.8	44.4	33.1	11.9	13.8
Japanese/Kuril		6.3	15.6	37.5	28.1	12.5	18.8
Japanese/Russian		0.0	6.3	35.9	35.9	21.9	21.9
Kuril/Russian		1.6	7.8	56.3	32.8	1.6	3.1
All Improve	95% Leaf Drop	2.5	6.9	65.0	16.3	9.4	11.9
Japanese/Kuril		12.5	18.8	21.9	21.9	25.0	37.5
Japanese/Russian		0.0	0.0	70.3	21.9	7.8	7.8
Kuril/Russian		0.0	7.8	81.3	7.8	3.1	3.1

[1]Comparisons made by pairwise comparison using linear contrasts extracted from mixed regression models (p<0.05).

9.3 Appendix C

Appendix C.1. Foundation Germplasm: Phenotypic average[1] +/- standard error for fruit yield and weight in blue honeysuckle and out-group comparison genotypes in 2012/2013 in the Fraser Valley, BC, Canada (n=18, J – Japanese, K – Kuril, R - Russian).

Genotype	Fruit Yield (g/plant)	Fruit Weight (g/fruit)
J-21-78	486.0 ± 68.7 l-o (8,8)	1.61 ± 0.06 l (6,6)
J-22-14	510.5 ± 103.6 l-o (4,4)	2.02 ± 0.08 n (9,9)
J-41-83	596.1 ± 116.3 no (1,1)	1.19 ± 0.03 ij (3,3)
J-42-45	498.0 ± 87.2 l-o (6,6)	1.08 ± 0.05 g-i (7,7)
J-43-87	577.1 ± 98.9 o (3,3)	1.14 ± 0.03 hi (2,2)
J-444-39	490.4 ± 80.4 k-n (7,7)	1.60 ± 0.06 l (4,4)
J-45-14	331.5 ± 49.1 j-m (10,10)	1.17 ± 0.04 i (10,10)
J-46-55	499.8 ± 88.3 l-o (5,5)	2.18 ± 0.10 o (8,8)
J-56-18	283.4 ± 30.6 j-l (11,11)	1.73 ± 0.04 m (11,11)
J-66-53	466.3 ± 70.1 l-o (9,9)	1.47 ± 0.07 k (5,5)
J-73-39	588.1 ± 83.9 m-o (2,2)	1.52 ± 0.07 kl (1,1)
K-3-03	204.4 ± 26.3 ij (14,2)	0.97 ± 0.03 e-g (14,2)
K-3-05	219.8 ± 33.5 i-k (13,1)	0.98 ± 0.02 e-g (13,1)
K-3-06	197.8 ± 33.5 hi (15,3)	0.98 ± 0.04 e-g (17,5)
K-3-07	185.3 ± 30.8 i (16,4)	0.97 ± 0.03 e-g (16,4)
K-97-12	185.0 ± 24.2 i (17,5)	1.30 ± 0.03 j (15,3)
R-2-06	32.9 ± 9.0 bc (25,9)	0.89 ± 0.05 de (26,10)
R-2-07	38.7 ± 8.3 cd (23,7)	0.63 ± 0.03 ab (23,7)
R-2-10	35.9 ± 7.0 bc (24,8)	0.73 ± 0.03 a-c (24,8)
R-2-11	32.3 ± 7.2 b (26,10)	0.81 ± 0.02 cd (25,9)
R-2-13	9.8 ± 3.0 a (28,12)	0.61 ± 0.04 a (28,12)
R-2-14	43.2 ± 13.5 bc (22,6)	0.76 ± 0.07 b-d (22,6)
R-2-16	27.3 ± 6.4 b (27,11)	0.63 ± 0.02 ab (27,11)
R-27-35	280.0 ± 52.9 i-k (12,1)	0.96 ± 0.04 ef (12,1)

[1]Genotypes not connected by the same letter are statistically different (p < 0.05) based on linear contrasts extracted from linear mixed models. In brackets, overall rank followed by group rank (J-PP ranked with Japanese and U of S cultivars ranked with Russian group).

Appendix C.1. Continued. Foundation Germplasm: Phenotypic average[1] +/- standard error for fruit yield and weight in blue honeysuckle and out-group comparison genotypes in 2012/2013 in the Fraser Valley, BC, Canada (n=18, J – Japanese, K – Kuril, R - Russian).

Genotype	Fruit Yield (g/plant)	Fruit Weight (g/fruit)
J-PP	161.8 ± 36.3 gh (18,2)	0.70 ± 0.04 a-c (18,2)
'Borealis'	68.7 ± 16.8 ef (19,3)	1.05 ± 0.04 f-h (19,3)
'Tundra'	66.3 ± 9.5 de (21,5)	1.01 ± 0.03 fg (20,4)
'Indigo Gem'	126.4 ± 22.6 fg (20,4)	1.04 ± 0.04 f-h (21,5)

[1]Genotypes not connected by the same letter are statistically different ($p < 0.05$) based on linear contrasts extracted from linear mixed models. In brackets, overall rank followed by group rank (J-PP ranked with Japanese and U of S cultivars ranked with Russian group).

Appendix C.2. Foundation Germplasm: Phenotypic average[1] +/- standard error and rankings for fruit length and width in blue honeysuckle and out-group comparison genotypes in 2012/2013 in the Fraser Valley, BC, Canada (n=18, J – Japanese, K – Kuril, R - Russian).

Genotype	Fruit Length (mm)	Fruit Width (mm)
J-21-78	21.97 ± 0.32 kl (4,4)	13.36 ± 0.23 jk (4,3)
J-22-14	24.86 ± 0.54 m (2,2)	14.38 ± 0.27 l (2,2)
J-41-83	19.50 ± 0.41 gh (9,8)	12.05 ± 0.10 gh (14,7)
J-42-45	17.29 ± 0.49 b-f (12,11)	11.46 ± 0.20 ef (22,11)
J-43-87	17.75 ± 0.26 ef (11,10)	11.79 ± 0.13 fg (19,10)
J-444-39	20.54 ± 0.41 i (5,5)	13.10 ± 0.24 j (11,6)
J-45-14	17.92 ± 0.32 f (10,9)	12.06 ± 0.14 gh (17,8)
J-46-55	26.41 ± 0.61 n (1,1)	14.21 ± 0.22 l (1,1)
J-56-18	20.93 ± 0.37 ij (3,3)	13.69 ± 0.20 k (9,5)
J-66-53	21.60 ± 0.45 jk (7,7)	12.40 ± 0.15 hi (7,4)
J-73-39	17.82 ± 0.25 ef (6,6)	12.87 ± 0.21 ij (18,9)
K-3-03	16.31 ± 0.25 b (18,4)	11.18 ± 0.17 e (27,5)
K-3-05	16.48 ± 0.20 bc (16,2)	11.48 ± 0.17 ef (26,4)
K-3-06	16.53 ± 0.16 b-d (17,3)	11.32 ± 0.13 ef (25,3)
K-3-07	16.73 ± 0.29 b-d (19,5)	11.21 ± 0.08 e (24,2)
K-97-12	20.32 ± 0.35 hi (8,1)	13.40 ± 0.18 jk (12,1)
R-2-06	20.64 ± 0.58 i (21,5)	10.46 ± 0.25 cd (10,5)
R-2-07	22.92 ± 0.65 l (26,10)	8.78 ± 0.20 a (3,1)
R-2-10	21.85 ± 0.57 jk (24,8)	9.98 ± 0.26 bc (5,2)
R-2-11	19.29 ± 0.58 gh (22,6)	10.39 ± 0.23 cd (15,7)
R-2-13	14.76 ± 0.57 a (28,12)	9.51 ± 0.27 b (28,12)
R-2-14	21.20 ± 0.65 i-k (23,7)	9.55 ± 0.25 b (8,4)
R-2-16	20.32 ± 0.42 hi (27,11)	8.80 ± 0.17 a (13,6)
R-27-35	21.67 ± 0.34 jk (20,4)	10.57 ± 0.15 d (6,3)

[1]Genotypes not connected by the same letter are statistically different (p < 0.05) based on linear contrasts extracted from linear mixed models. In brackets, overall rank followed by group rank (J-PP ranked with Japanese and U of S cultivars ranked with Russian group).

Appendix C.2. Continued. Foundation Germplasm: Phenotypic average[1] +/- standard error for fruit length and width in blue honeysuckle and out-group comparison genotypes in 2012/2013 in the Fraser Valley, BC, Canada (n=18, J – Japanese, K – Kuril, R - Russian).

Genotype	Fruit Length (mm)	Fruit Width (mm)
J-PP	17.44 ± 0.38 c-f (25,9)	9.49 ± 0.21 b (21,10)
'Borealis'	16.87 ± 0.45 b-e (14,2)	11.41 ± 0.21 ef (20,9)
'Tundra'	19.23 ± 0.58 g (15,3)	11.84 ± 0.17 fg (16,8)
'Indigo Gem'	17.57 ± 0.65 d-f (13,1)	12.16 ± 0.38 gh (23,11)

[1]Genotypes not connected by the same letter are statistically different ($p < 0.05$) based on linear contrasts extracted from linear mixed models. In brackets, overall rank followed by group rank (J-PP ranked with Japanese and U of S cultivars ranked with Russian group).

Appendix C.3. Foundation Germplasm: Phenotypic average[1] +/- standard error for fruit size ratios in blue honeysuckle and out-group comparison genotypes in 2012/2013 in the Fraser Valley, BC, Canada (n=18, J – Japanese, K – Kuril, R - Russian).

Genotype	Fruit Length:Width	Fruit Length:Weight (mm/g)	Fruit Width:Weight (mm/g)
J-21-78	1.65 ± 0.02 g (5,4)	13.86 ± 0.40 bc (12,4)	8.43 ± 0.26 c (23,6)
J-22-14	1.74 ± 0.03 h (1,1)	12.53 ± 0.45 ab (11,3)	7.21 ± 0.21 ab (26,9)
J-41-83	1.62 ± 0.03 fg (11,9)	16.56 ± 0.40 d-g (13,5)	10.26 ± 0.23 d (16,1)
J-42-45	1.51 ± 0.03 b-e (15,11)	16.52 ± 0.69 d-g (17,8)	11.11 ± 0.66 de (17,2)
J-43-87	1.51 ± 0.02 b-d (13,10)	15.62 ± 0.26 c-f (18,9)	10.41 ± 0.25 d (20,3)
J-444-39	1.57 ± 0.03 d-f (6,5)	13.03 ± 0.34 ab (15,6)	8.33 ± 0.25 c (24,7)
J-45-14	1.49 ± 0.02 bc (10,8)	15.48 ± 0.30 c-e (21,10)	10.45 ± 0.24 d (21,4)
J-46-55	1.87 ± 0.04 i (2,2)	12.55 ± 0.73 ab (7,1)	6.76 ± 0.36 a (25,8)
J-56-18	1.53 ± 0.03 c-e (3,3)	12.15 ± 0.26 ab (16,7)	7.96 ± 0.19 bc (27,10)
J-66-53	1.75 ± 0.03 h (8,7)	15.06 ± 0.51 cd (10,2)	8.68 ± 0.31 c (22,5)
J-73-39	1.38 ± 0.02 a (7,6)	11.54 ± 0.31 a (28,11)	8.38 ± 0.25 c (28,11)
K-3-03	1.47 ± 0.02 bc (19,5)	16.99 ± 0.38 e-h (24,4)	11.69 ± 0.37 e-g (13,3)
K-3-05	1.44 ± 0.02 ab (14,2)	16.86 ± 0.37 e-h (27,5)	11.74 ± 0.26 e-g (15,4)
K-3-06	1.47 ± 0.02 bc (17,3)	17.30 ± 0.70 f-h (23,3)	11.86 ± 0.51 e-g (12,2)
K-3-07	1.49 ± 0.02 bc (18,4)	17.42 ± 0.32 gh (20,2)	11.72 ± 0.29 e-g (11,1)
K-97-12	1.50 ± 0.02 b-e (4,1)	15.85 ± 0.21 d-g (19,1)	10.58 ± 0.23 d (19,5)
R-2-06	1.97 ± 0.04 j (21,5)	24.14 ± 0.89 ij (6,6)	12.35 ± 0.39 f-h (7,7)
R-2-07	2.62 ± 0.04 m (28,12)	37.51 ± 1.37 n (1,1)	14.45 ± 0.62 k (1,1)
R-2-10	2.18 ± 0.05 k (23,7)	31.08 ± 1.03 lm (4,4)	14.31 ± 0.46 jk (3,3)
R-2-11	1.82 ± 0.04 hi (22,6)	23.49 ± 0.36 i (9,8)	12.98 ± 0.21 hi (8,8)
R-2-13	1.46 ± 0.07 a-c (25,9)	26.39 ± 2.85 jk (25,11)	18.23 ± 1.63 l (5,5)
R-2-14	2.25 ± 0.08 kl (24,8)	28.77 ± 2.54 kl (3,3)	12.80 ± 0.99 g-j (4,4)
R-2-16	2.31 ± 0.02 l (27,11)	33.06 ± 0.95 m (2,2)	14.43 ± 0.43 k (2,2)
R-27-35	2.06 ± 0.03 j (20,4)	23.10 ± 0.87 i (5,5)	11.23 ± 0.37 d-f (9,9)

[1]Genotypes not connected by the same letter are statistically different ($p < 0.05$) based on linear contrasts extracted from linear mixed models. In brackets, overall rank followed by group rank (J-PP ranked with Japanese and U of S cultivars ranked with Russian group).

Appendix C.3. Continued. Foundation Germplasm: Phenotypic average[1] +/- standard error for fruit length:width, length:weight and width:weight in blue honeysuckle and out-group comparison genotypes in 2012/2013 in the Fraser Valley, BC, Canada (n=18, J – Japanese, K – Kuril, R - Russian).

Genotype	Fruit Length:Width	Fruit Length:Weight (mm/g)	Fruit Width:Weight (mm/g)
J-PP	1.86 ± 0.02 i (26,10)	25.73 ± 1.02 j (8,7)	13.89 ± 0.59 i-k (6,6)
'Borealis'	1.48 ± 0.03 bc (9,1)	16.49 ± 0.47 d-g (26,12)	11.22 ± 0.33 d-f (14,11)
'Tundra'	1.59 ± 0.04 e-g (12,2)	18.80 ± 0.24 h (14,9)	11.96 ± 0.38 e-h (10,10)
'Indigo Gem'	1.45 ± 0.05 ab (16,3)	16.92 ± 0.34 d-h (22,10)	11.89 ± 0.44 e-h (18,12)

[1]Genotypes not connected by the same letter are statistically different ($p < 0.05$) based on linear contrasts extracted from linear mixed models. In brackets, overall rank followed by group rank (J-PP ranked with Japanese and U of S cultivars ranked with Russian group).

Appendix C.4. Foundation Germplasm: Comparisons of blue honeysuckle parent genotypes used in each hybrid cross combination to generate improved seedling families for traits related to agronomic potential in 2012/2013 in Chilliwack, BC, Canada (based on linear contrasts extracted from linear mixed model regression, $p < 0.05$, n=6).

		Kuril vs. Japanese	Japanese vs. Russian	Russian vs. Kuril			Kuril vs. Japanese	Japanese vs. Russian	Russian vs. Kuril
Fruit Yield	Lower	1	8	6	Fruit Length:Width	Lower	2	2	0
	Equal	7	8	10		Equal	5	1	3
	Greater	0	0	0		Greater	1	13	13
Fruit Weight	Lower	7	16	11	Fruit Length:Weight	Lower	0	0	0
	Equal	0	0	5		Equal	1	0	2
	Greater	1	0	0		Greater	7	16	14
Fruit Length	Lower	7	7	4	Fruit Width:Weight	Lower	0	0	0
	Equal	0	6	1		Equal	1	0	4
	Greater	1	3	11		Greater	7	16	12
Fruit Width	Lower	7	16	12					
	Equal	0	0	4					
	Greater	1	0	0					

Appendix C.5. Improved Germplasm: Statistical classification (%) of blue honeysuckle hybrids compared with their parent foundation genotypes for fruit morphological traits in 2012/2013 in Chilliwack, BC, Canada (n=6).

		Low			High		Total
		Transgressive Segregants	Parent Types	Intermediates	Parent Types	Transgressive Segregants	Transgressive Segregants
All Improved	Fruit Yield	4.4	11.3	55.0	25.6	3.8	8.1
Japanese/Kuril		3.1	6.3	75.0	9.4	6.3	9.4
Japanese/Russian		1.6	9.4	46.9	40.6	1.6	3.1
Kuril/Russian		7.8	15.6	53.1	18.8	4.7	12.5
All Improved	Fruit Weight	2.5	9.4	48.1	23.8	16.3	18.8
Japanese/Kuril		3.1	12.5	28.1	31.3	25.0	28.1
Japanese/Russian		0.0	1.6	79.7	14.1	4.7	4.7
Kuril/Russian		4.7	15.6	26.6	29.7	23.4	28.1
All Improved	Fruit Length	9.4	18.1	21.3	29.4	21.9	31.3
Japanese/Kuril		9.4	18.8	18.8	37.5	15.6	25.0
Japanese/Russian		17.2	20.3	20.3	18.8	23.4	40.6
Kuril/Russian		1.6	15.6	23.4	35.9	23.4	25.0
All Improved	Fruit Width	3.8	10.0	43.1	29.4	13.8	17.5
Japanese/Kuril		3.1	34.4	43.8	18.8	0.0	3.1
Japanese/Russian		0.0	4.7	71.9	17.2	6.3	6.3
Kuril/Russian		7.8	20.3	18.8	34.4	18.8	26.6

		Low			High		Total
		Transgressive Segregants	Parent Types	Intermediates	Parent Types	Transgressive Segregants	Transgressive Segregants
All Improved	Fruit Length: Width	11.9	19.4	36.9	11.3	20.6	32.5
Japanese/Kuril		21.9	31.3	15.6	6.3	25.0	46.9
Japanese/Russian		18.8	17.2	39.1	3.1	21.9	40.6
Kuril/Russian		0.0	15.6	45.3	21.9	17.2	17.2
All Improved	Fruit Length: Weight	7.5	24.4	55.6	10.0	2.5	10.0
Japanese/Kuril		12.5	53.1	21.9	12.5	0.0	12.5
Japanese/Russian		6.3	17.2	76.6	0.0	0.0	6.3
Kuril/Russian		6.3	17.2	51.6	18.8	6.3	12.5
All Improved	Fruit Width: Weight	9.4	34.4	40.6	11.9	3.8	13.1
Japanese/Kuril		15.6	37.5	25.0	15.6	6.3	21.9
Japanese/Russian		1.6	34.4	57.8	6.3	0.0	1.6
Kuril/Russian		14.1	32.8	31.3	15.6	6.3	20.3

[1]Comparisons made by pairwise comparison using linear contrasts extracted from mixed regression models (p<0.05).

Appendix C.6. Foundation and Improved Germplasm: Diversity of unique 1° and 2° fruit shapes in blue honeysuckle in 2012/2013 in the Fraser Valley, BC, Canada.

Unique Fruit Shape Combinations	Japanese	Kuril	Russian	Japanese/Kuril	Japanese/Russian	Kuril/Russian	All Foundation	All Improved	All Foundation & Improved
Primarily ovate & some torpedo					1			1	1
Primarily ovate & some torpedo & oblong				1	1			2	2
Primarily ovate & some torpedo & cylindrical				1				1	1
Primarily ovate & some oblong				1				1	1
Primarily ovate & some cylindrical				1				1	1
Primarily ovate & some cylindrical & oblong	1			5	2		1	7	8
Ovate & torpedo				1				1	1
Primarily ovate & torpedo & some bottle				1				1	1
Primarily ovate & torpedo & some oblong	2			1			2	1	3
Ovate & oblong	1				1		1	1	2
Primarily ovate & oblong & some spindle			1				1		1
Ovate & cylindrical					1			1	1
Primarily ovate & cylindrical & some oblong	1	1		1	4	3	2	8	10
Primarily ovate & cylindrical & some bottle						1		1	1
Primarily torpedo & some ovate & oblong				1		1		2	2
Primarily torpedo & some oblong					2			2	2
Primarily torpedo & some cylindrical & bottle	1						1		1
Torpedo & oblong					1			1	1
Primarily torpedo & oblong & some ovate						1		1	1
Primarily torpedo & oblong & some pod				1				1	1
Oblong			2		1	2	2	3	5
Primarily oblong & some ovate & torpedo				1				1	1
Primarily oblong & some ovate & cylindrical				1				1	1
Primarily oblong & some ovate & pear				1				1	1
Primarily oblong & some ovate & bottle					1			1	1
Primarily oblong & some cylindrical					4	1		5	5
Primarily oblong & some cylindrical & pear					1	1		2	2

Appendix C.6. Continued. Foundation and Improved Germplasm: Diversity of unique $1°$ and $2°$ fruit shapes in blue honeysuckle in 2012/2013 in the Fraser Valley, BC, Canada.

Unique Fruit Shape Combinations	Japanese	Kuril	Russian	Japanese/Kuril	Japanese/Russian	Kuril/Russian	All Foundation	All Improved	All Foundation & Improved
Primarily oblong & some cylindrical & bottle					1	3		4	4
Primarily oblong & some bell						2		2	2
Primarily oblong & some bell & pear						1		1	1
Primarily oblong & some bell & bottle					1	1		2	2
Primarily oblong & some pear			1		2	1	1	3	4
Primarily oblong & some bottle			1				1		1
Oblong & cylindrical				3	2	7		12	12
Primarily oblong & cylindrical & some ovate	4			3	2	3	4	8	12
Primarily oblong & cylindrical & some torpedo					1			1	1
Primarily oblong & cylindrical & some bell				1		1		2	2
Primarily oblong & cylindrical & some pear				1	2	1		4	4
Oblong & bottle					2	2		4	4
Primarily oblong & bottle & some ovate					1			1	1
Primarily oblong & bottle & some cylindrical					2	1		3	3
Primarily oblong & bottle & some spindle	1						1		1
Oblong & pear					1	2		3	3
Primarily oblong & pear & some cylindrical					1			1	1
Primarily cylindrical & some ovate					1			1	1
Primarily cylindrical & some ovate & oblong				2	1			3	3
Primarily cylindrical & some ovate & bottle				1	1			2	2
Primarily cylindrical & some torpedo & oblong					1			1	1
Primarily cylindrical & some oblong				1	2	2		5	5
Primarily cylindrical & some oblong & bell					1			1	1
Primarily cylindrical & some oblong & pear						1		1	1
Primarily cylindrical & some oblong & bottle					1	1		2	2
Primarily cylindrical & some bell & pear					1			1	1

Appendix C.6. Continued. Foundation and Improved Germplasm: Diversity of unique 1° and 2° fruit shapes in blue honeysuckle in 2012/2013 in the Fraser Valley, BC, Canada.

Unique Fruit Shape Combinations	Japanese	Kuril	Russian	Japanese/Kuril	Japanese/Russian	Kuril/Russian	All Foundation	All Improved	All Foundation & Improved
Primarily cylindrical & some bell & bottle					1			1	1
Primarily cylindrical & some pear				1				1	1
Primarily cylindrical & some bottle				1	1			2	2
Primarily cylindrical & oblong & some bottle	2			1	2	4	2	7	9
Primarily cylindrical & bell & some pear						1		1	1
Cylindrical & bottle					1	6		7	7
Primarily cylindrical & bottle & some ovate	1						1		1
Primarily cylindrical & bottle & some oblong					1	2		3	3
Bell						1		1	1
Primarily bell & some bottle			1				1		1
Primarily bell & pear & some oblong						1		1	1
Bell & bottle					1			1	1
Primarily pear & some ovate & oblong						1		1	1
Primarily pear & some oblong					1			1	1
Primarily pear & some bottle					1			1	1
Primarily pear & some spindle					1			1	1
Bottle						3		3	3
Primarily bottle & some ovate & bell					1			1	1
Primarily bottle & some oblong			1		2		1	2	3
Primarily bottle & some oblong & cylindrical					1			1	1
Primarily bottle & some cylindrical	1						1		1
Primarily bottle & some bell					2			2	2
Primarily bottle & some spindle						1		1	1
Primarily spindle & some bottle			1				1		1
Total Number of Genotypes	11	5	8	32	64	59	24	155	179
Total Number of Unique Shape Combinations	10	2	7	23	46	31	17	70	77

Appendix C.7. Foundation and Improved Germplasm: Diversity and frequency of genotypes with unique combinations of proximal fruit end shapes in blue honeysuckle groups in 2012/2013 in the Fraser Valley, BC, Canada.

Unique Proximal End Fruit Shape Combinations	Japanese	Kuril	Russian	Japanese/Kuril	Japanese/Russian	Kuril/Russian	All Foundation	All Improved	All Foundation & Improved
Primarily acute & some rounded					1			1	1
Acute & rounded			5	2	6	1	5	9	14
Primarily acute & rounded & some truncate					2			2	2
Rounded			2		5	13	2	18	20
Primarily rounded & some acute				1	1	2		4	4
Primarily rounded & some truncate				1	9	8		18	18
Rounded & truncated	5	5	1	11	20	18	11	49	60
Primarily rounded & truncated & some acute					2			2	2
Truncated	3			7	6	10	3	23	26
Primarily truncated & some rounded	3			10	12	7	3	29	32
Total Number of Gentoypes	11	5	8	32	64	59	24	155	179
Total Number of Unique Shape Combinations	3	1	3	6	12	7	5	12	12

Appendix C.8. Foundation and Improved Germplasm: Diversity of unique combinations of distal fruit end shapes in blue honeysuckle groups in 2012/2013 in the Fraser Valley, BC, Canada.

Unique Distal End Fruit Shape Combinations	Japanese	Kuril	Russian	Japanese/Kuril	Japanese/Russian	Kuril/Russian	All Foundation	All Improved	All Foundation & Improved
Primarily flat & some indented				1				1	1
Primarily flat & some rounded & indented					1			1	1
Primarily flat & some rounded				1	3	1		5	5
Flat & rounded		1		3	2	8	1	13	14
Flat & rounded & some indented				2	1	2		5	5
Primarily flat & rounded & some peaked					1			1	1
Flat & indented				1	2	1		4	4
Primarily flat & indented & some rounded	1				3	3	1	6	7
Rounded			2	2	3	4	2	9	11
Primarily rounded & some flat	1			5	5	4	1	14	15
Primarily rounded & some flat & indented	1				3	3	1	6	7
Primarily rounded & some indented				2	4	5		11	11
Primarily rounded & some indented & peaked				1				1	1
Primarily rounded & some peaked				1	2	1		4	4
Primarily rounded & indented	3	4		3	14	10	7	27	34
Primarily rounded & indented & some flat	1						1		1
Primarily rounded & indented & some peaked					1			1	1
Rounded & peaked	1		1	4	3	2	2	9	11
Primarily rounded & peaked & some flat	1						1		1
Primarily rounded & peaked & some indented			2	1	1		2	2	4

Appendix C.8. Continued. Foundation and Improved Germplasm: Diversity of unique combinations of distal fruit end shapes in blue honeysuckle groups in 2012/2013 in the Fraser Valley, BC, Canada.

Unique Distal End Fruit Shape Combinations	Japanese	Kuril	Russian	Japanese/Kuril	Japanese/Russian	Kuril/Russian	All Foundation	All Improved	All Foundation & Improved
Indented	1		2		5	10	3	15	18
Primarily indented & some flat					1			1	1
Primarily indented & some rounded			1	4	5	4	1	13	14
Primarily indented & some rounded & peaked					2			2	2
Primarily peaked & some flat & indented	1						1		1
Primarily peaked & some rounded				1	2	1		4	4
Total Number of Genotypes	11	5	8	32	64	59	24	155	179
Total Number of Unique Shape Combinations	9	2	6	15	21	15	13	23	26

Appendix C.9. Foundation Germplasm: Phenotypic average +/- standard error for fruit morphological ratings of agronomic potential in blue honeysuckle and out-group comparisons in 2012/2013 in the Fraser Valley, BC, Canada (n=18, J – Japanese, K – Kuril, R – Russian).

Genotype (Scale)	Fruit Synanthy (1-2)	Fruit Surface (1-5)	Fruit Pubescence (1-9)	Fruit Bloom (1-7)	Fruit Colour (1-3)
J-21-78	1.44 ± 0.18	4.56 ± 0.24	1.00 ± 0.00	2.00 ± 0.24	1.67 ± 0.17
J-22-14	1.38 ± 0.18	2.89 ± 0.20	1.00 ± 0.00	2.11 ± 0.31	1.38 ± 0.18
J-41-83	1.11 ± 0.11	1.56 ± 0.18	1.22 ± 0.22	2.44 ± 0.56	2.22 ± 0.22
J-42-45	1.56 ± 0.18	1.89 ± 0.20	2.44 ± 0.29	1.67 ± 0.37	1.67 ± 0.17
J-43-87	1.78 ± 0.15	2.00 ± 0.00	2.44 ± 0.29	1.22 ± 0.15	1.67 ± 0.24
J-444-39	1.56 ± 0.18	1.78 ± 0.15	1.44 ± 0.29	1.56 ± 0.24	2.00 ± 0.17
J-45-14	1.33 ± 0.17	1.89 ± 0.11	1.00 ± 0.00	3.44 ± 0.50	2.67 ± 0.17
J-46-55	1.44 ± 0.18	2.00 ± 0.00	1.44 ± 0.29	3.78 ± 0.32	2.33 ± 0.17
J-56-18	1.67 ± 0.17	2.38 ± 0.18	2.33 ± 0.33	1.44 ± 0.18	1.44 ± 0.24
J-66-53	1.78 ± 0.15	2.89 ± 0.11	1.00 ± 0.00	2.56 ± 0.34	2.89 ± 0.11
J-73-39	1.38 ± 0.18	1.00 ± 0.00	1.22 ± 0.22	2.56 ± 0.47	1.89 ± 0.20
K-3-03	1.11 ± 0.11	1.78 ± 0.15	1.89 ± 0.35	4.44 ± 0.38	1.56 ± 0.18
K-3-05	1.11 ± 0.11	1.67 ± 0.17	2.78 ± 0.22	3.78 ± 0.32	1.33 ± 0.17
K-3-06	1.00 ± 0.00	1.67 ± 0.17	2.22 ± 0.32	4.22 ± 0.46	1.44 ± 0.18
K-3-07	1.00 ± 0.00	1.78 ± 0.15	2.44 ± 0.29	4.33 ± 0.37	1.22 ± 0.15
K-97-12	1.50 ± 0.22	1.67 ± 0.21	9.00 ± 0.00	1.83 ± 0.17	1.60 ± 0.24
R-2-06	1.67 ± 0.21	3.17 ± 0.40	1.00 ± 0.00	1.00 ± 0.00	1.33 ± 0.21
R-2-07	1.00 ± 0.00	5.00 ± 0.00	1.22 ± 0.22	1.00 ± 0.00	1.00 ± 0.00
R-2-10	1.00 ± 0.00	2.80 ± 0.37	1.00 ± 0.00	2.00 ± 0.32	1.40 ± 0.24
R-2-11	1.86 ± 0.14	2.14 ± 0.26	1.00 ± 0.00	1.57 ± 0.20	1.29 ± 0.18
R-2-13	1.67 ± 0.33	1.00 ± 0.00	3.67 ± 1.33	2.00 ± 0.58	1.00 ± 0.00
R-2-14	1.67 ± 0.33	3.67 ± 0.33	2.33 ± 0.67	1.33 ± 0.33	1.00 ± 0.00
R-2-16	1.17 ± 0.17	3.00 ± 0.37	3.00 ± 0.52	1.00 ± 0.00	1.00 ± 0.00
R-27-35	1.11 ± 0.11	3.56 ± 0.34	3.44 ± 0.56	2.44 ± 0.34	2.56 ± 0.24
J-PP	1.11 ± 0.11	1.56 ± 0.18	1.00 ± 0.00	2.89 ± 0.31	2.33 ± 0.24
'Borealis'	1.63 ± 0.18	2.13 ± 0.35	8.00 ± 0.00	3.22 ± 0.32	2.33 ± 0.24
'Tundra'	1.67 ± 0.21	2.33 ± 0.21	7.00 ± 0.00	2.17 ± 0.31	1.17 ± 0.17
'Indigo Gem'	1.43 ± 0.20	1.57 ± 0.20	7.00 ± 0.00	3.86 ± 0.40	1.00 ± 0.00

Appendix C.9. Continued. Foundation Germplasm: Phenotypic average +/- standard error for fruit morphological ratings of agronomic potential in blue honeysuckle and out-group comparisons in 2012/2013 in the Fraser Valley, BC, Canada (n=18, J – Japanese, K – Kuril, R – Russian).

Genotype (Scale)	Fruit Shape in Cross-Section (1-5)	Distal Opening Size (1-7)	Hetero-geneity of Size (1-5)	Hetero-eneity of Shape (1-5)	Fruit Taste (1-6)	Fruit Aroma (1-7)
J-21-78	2.11 ± 0.31	4.22 ± 0.28	3.17 ± 0.17	3.06 ± 0.15	3.11 ± 0.41	2.89 ± 0.18
J-22-14	2.22 ± 0.32	3.63 ± 0.50	3.06 ± 0.22	2.89 ± 0.18	5.00 ± 0.54	2.53 ± 0.12
J-41-83	3.44 ± 0.34	1.89 ± 0.11	3.61 ± 0.14	3.17 ± 0.19	3.39 ± 0.49	3.17 ± 0.17
J-42-45	2.22 ± 0.15	1.78 ± 0.15	2.94 ± 0.25	2.83 ± 0.28	4.44 ± 0.58	3.89 ± 0.21
J-43-87	2.67 ± 0.17	1.89 ± 0.11	3.11 ± 0.18	2.78 ± 0.24	4.22 ± 0.45	3.88 ± 0.34
J-444-39	2.56 ± 0.24	4.00 ± 0.53	3.22 ± 0.13	3.11 ± 0.21	5.33 ± 0.48	5.24 ± 0.26
J-45-14	2.56 ± 0.18	3.00 ± 0.44	2.89 ± 0.18	2.56 ± 0.20	2.67 ± 0.40	2.06 ± 0.13
J-46-55	1.67 ± 0.29	4.22 ± 0.32	3.39 ± 0.16	3.11 ± 0.21	3.33 ± 0.44	2.39 ± 0.16
J-56-18	1.89 ± 0.20	4.78 ± 0.22	4.00 ± 0.24	3.89 ± 0.25	3.56 ± 0.30	2.89 ± 0.16
J-66-53	2.78 ± 0.32	2.00 ± 0.00	3.11 ± 0.14	3.00 ± 0.11	5.00 ± 0.59	4.61 ± 0.38
J-73-39	2.25 ± 0.25	1.50 ± 0.19	3.24 ± 0.20	3.06 ± 0.33	4.94 ± 0.51	4.12 ± 0.19
K-3-03	4.00 ± 0.33	1.00 ± 0.00	2.61 ± 0.26	2.56 ± 0.32	3.17 ± 0.23	3.89 ± 0.24
K-3-05	4.44 ± 0.29	1.00 ± 0.00	2.67 ± 0.21	2.83 ± 0.22	3.11 ± 0.18	3.94 ± 0.22
K-3-06	4.56 ± 0.18	1.11 ± 0.11	2.33 ± 0.23	2.61 ± 0.28	3.06 ± 0.26	4.11 ± 0.24
K-3-07	4.33 ± 0.17	1.33 ± 0.24	2.22 ± 0.27	2.35 ± 0.28	3.06 ± 0.26	3.76 ± 0.20
K-97-12	3.83 ± 0.17	1.00 ± 0.00	3.73 ± 0.27	2.87 ± 0.17	4.47 ± 0.58	2.73 ± 0.15
R-2-06	2.50 ± 0.50	5.83 ± 0.40	2.47 ± 0.26	2.60 ± 0.21	4.77 ± 0.60	3.58 ± 0.65
R-2-07	1.56 ± 0.29	5.11 ± 0.63	3.06 ± 0.17	3.78 ± 0.21	2.22 ± 0.32	3.39 ± 0.29
R-2-10	3.40 ± 0.75	5.40 ± 0.40	3.57 ± 0.20	3.69 ± 0.17	4.15 ± 0.37	2.36 ± 0.25
R-2-11	2.86 ± 0.26	1.00 ± 0.00	3.44 ± 0.26	3.38 ± 0.20	4.27 ± 0.50	3.07 ± 0.27
R-2-13	1.33 ± 0.33	1.00 ± 0.00	3.25 ± 0.28	2.75 ± 0.39	6.38 ± 0.63	4.17 ± 0.31
R-2-14	3.67 ± 0.67	5.33 ± 0.88	2.78 ± 0.22	2.78 ± 0.22	6.14 ± 0.55	3.43 ± 0.30
R-2-16	1.67 ± 0.42	5.67 ± 0.33	2.87 ± 0.17	3.00 ± 0.22	2.93 ± 0.30	1.62 ± 0.18
R-27-35	2.56 ± 0.47	1.11 ± 0.11	3.11 ± 0.14	3.50 ± 0.15	3.22 ± 0.30	3.50 ± 0.26
J-PP	3.22 ± 0.28	2.63 ± 0.46	3.06 ± 0.16	3.47 ± 0.17	4.44 ± 0.58	4.19 ± 0.28
'Borealis'	2.44 ± 0.24	4.00 ± 0.82	2.94 ± 0.24	3.22 ± 0.19	4.27 ± 0.54	3.71 ± 0.22
'Tundra'	2.67 ± 0.21	3.83 ± 1.28	3.20 ± 0.24	2.93 ± 0.25	3.53 ± 0.52	4.00 ± 0.31
'Indigo Gem'	1.29 ± 0.29	1.43 ± 0.20	3.44 ± 0.18	3.31 ± 0.24	3.60 ± 0.47	3.60 ± 0.42

Appendix C.9. Continued. Foundation Germplasm: Phenotypic average +/- standard error for fruit morphological ratings of agronomic potential in blue honeysuckle and out-group comparisons in 2012/2013 in the Fraser Valley, BC, Canada (n=18, J – Japanese, K – Kuril, R – Russian).

Genotype (Scale)	Fruit Mold (1-4)	Fruit Flesh Firmness (1-7)	Strength of Attachment (1-9)	Stem Retention in Harvest (1-7)	Picking Scar Quality (1-4)
J-21-78	1.33 ± 0.24	4.11 ± 0.18	2.11 ± 0.35	1.11 ± 0.11	3.06 ± 0.06
J-22-14	1.11 ± 0.11	3.12 ± 0.28	3.41 ± 0.36	1.56 ± 0.20	1.44 ± 0.18
J-41-83	1.11 ± 0.11	2.39 ± 0.28	5.44 ± 0.25	4.94 ± 0.24	1.17 ± 0.09
J-42-45	1.00 ± 0.00	2.50 ± 0.31	3.17 ± 0.35	2.28 ± 0.24	1.11 ± 0.11
J-43-87	1.00 ± 0.00	2.41 ± 0.31	2.61 ± 0.39	1.72 ± 0.28	1.22 ± 0.13
J-444-39	1.22 ± 0.22	4.56 ± 0.33	6.94 ± 0.36	4.44 ± 0.47	1.44 ± 0.23
J-45-14	1.00 ± 0.00	3.39 ± 0.20	3.47 ± 0.42	2.61 ± 0.24	1.17 ± 0.12
J-46-55	1.11 ± 0.11	3.78 ± 0.30	6.17 ± 0.34	2.39 ± 0.29	3.28 ± 0.11
J-56-18	3.00 ± 0.44	4.50 ± 0.22	3.67 ± 0.23	1.39 ± 0.18	1.61 ± 0.22
J-66-53	1.00 ± 0.00	2.67 ± 0.32	3.06 ± 0.42	2.67 ± 0.24	1.78 ± 0.24
J-73-39	1.11 ± 0.11	4.39 ± 0.37	7.44 ± 0.38	4.00 ± 0.30	1.35 ± 0.12
K-3-03	1.56 ± 0.34	3.33 ± 0.26	5.33 ± 0.27	4.22 ± 0.44	1.89 ± 0.08
K-3-05	1.67 ± 0.33	3.33 ± 0.28	5.78 ± 0.30	3.89 ± 0.37	1.83 ± 0.09
K-3-06	1.89 ± 0.39	3.61 ± 0.23	5.44 ± 0.39	3.89 ± 0.36	1.83 ± 0.09
K-3-07	1.67 ± 0.33	3.22 ± 0.17	5.59 ± 0.34	3.67 ± 0.34	2.00 ± 0.00
K-97-12	1.67 ± 0.29	2.47 ± 0.36	4.73 ± 0.36	1.53 ± 0.24	1.13 ± 0.13
R-2-06	1.00 ± 0.00	2.38 ± 0.24	6.60 ± 0.39	3.80 ± 0.55	3.14 ± 0.18
R-2-07	1.00 ± 0.00	2.56 ± 0.32	4.61 ± 0.31	1.89 ± 0.28	1.89 ± 0.23
R-2-10	1.00 ± 0.00	1.71 ± 0.19	5.50 ± 0.40	2.07 ± 0.47	2.00 ± 0.26
R-2-11	1.00 ± 0.00	2.93 ± 0.37	6.31 ± 0.34	3.69 ± 0.38	1.19 ± 0.14
R-2-13	1.00 ± 0.00	2.43 ± 0.37	5.50 ± 0.34	2.58 ± 0.31	1.25 ± 0.18
R-2-14	1.00 ± 0.00	2.83 ± 0.54	3.75 ± 0.53	2.13 ± 0.35	1.50 ± 0.19
R-2-16	1.00 ± 0.00	2.14 ± 0.23	5.47 ± 0.24	2.53 ± 0.29	1.00 ± 0.00
R-27-35	1.33 ± 0.24	5.44 ± 0.26	7.39 ± 0.22	3.72 ± 0.36	3.89 ± 0.11
J-PP	1.00 ± 0.00	4.69 ± 0.22	7.06 ± 0.30	2.61 ± 0.35	1.35 ± 0.12
'Borealis'	1.00 ± 0.00	5.86 ± 0.29	6.94 ± 0.29	4.17 ± 0.41	3.22 ± 0.25
'Tundra'	1.00 ± 0.00	2.27 ± 0.33	6.00 ± 0.29	1.40 ± 0.21	1.80 ± 0.26
'Indigo Gem'	1.22 ± 0.22	4.67 ± 0.32	5.75 ± 0.31	1.63 ± 0.22	2.00 ± 0.29

Appendix C.10. Foundation Germplasm: Relative selection index of 16 range standardized morphological traits related to agronomic potential in blue honeysuckle in 2012/2013 in the Fraser Valley, BC, Canada (n=18, J – Japanese, K – Kuril, R – Russian).

Genotype	Fruit Synanthy	Fruit Surface	Fruit Pubescence	Fruit Bloom	Fruit Colour	Fruit Shape in Cross-Section	Distal Opening Size	Heterogeneity of Fruit Size	Heterogeneity of Fruit Shape
J-21-78	*-0.02*	*-0.44*	0.18	0.06	*-0.00*	0.13	*-0.19*	*-0.02*	*-0.00*
J-22-14	0.01	*-0.11*	0.18	0.04	0.09	0.10	*-0.11*	0.01	0.03
J-41-83	0.14	0.16	0.16	*-0.00*	*-0.19*	*-0.14*	0.14	*-0.10*	*-0.03*
J-42-45	*-0.08*	0.09	0.02	0.11	*-0.00*	0.10	0.16	0.03	0.04
J-43-87	*-0.19*	0.07	0.02	0.17	*-0.00*	0.01	0.14	*-0.00*	0.05
J-444-39	*-0.08*	0.11	0.14	0.12	*-0.11*	0.04	*-0.16*	*-0.03*	*-0.01*
J-45-14	0.03	0.09	0.18	*-0.15*	*-0.34*	0.04	*-0.02*	0.04	0.10
J-46-55	*-0.02*	0.07	0.14	*-0.19*	*-0.23*	0.21	*-0.19*	*-0.06*	*-0.01*
J-56-18	*-0.14*	*-0.01*	0.04	0.14	0.07	0.17	*-0.27*	*-0.18*	*-0.17*
J-66-53	*-0.19*	*-0.11*	0.18	*-0.02*	*-0.41*	*-0.01*	0.13	*-0.00*	0.01
J-73-39	0.01	0.27	0.16	*-0.02*	*-0.08*	0.10	0.20	*-0.03*	*-0.00*
K-3-03	0.14	0.11	0.09	*-0.29*	0.03	*-0.25*	0.27	0.10	0.10
K-3-05	0.14	0.13	*-0.01*	*-0.19*	0.11	*-0.34*	0.27	0.08	0.04
K-3-06	0.20	0.13	0.05	*-0.26*	0.07	*-0.36*	0.25	0.15	0.09
K-3-07	0.20	0.11	0.02	*-0.27*	0.14	*-0.32*	0.22	0.17	0.14
K-97-12	*-0.05*	0.13	*-0.70*	0.08	0.02	*-0.22*	0.27	*-0.13*	0.03
R-2-06	*-0.14*	*-0.17*	0.18	0.20	0.11	0.05	*-0.42*	0.12	0.09
R-2-07	0.20	*-0.53*	0.16	0.20	0.22	0.24	*-0.32*	0.01	*-0.15*
R-2-10	0.20	*-0.09*	0.18	0.06	0.09	*-0.13*	*-0.36*	*-0.10*	*-0.13*
R-2-11	*-0.23*	0.04	0.18	0.12	0.12	*-0.02*	0.27	*-0.07*	*-0.07*
R-2-13	*-0.14*	0.27	*-0.11*	0.06	0.22	0.28	0.27	*-0.03*	0.06
R-2-14	*-0.14*	*-0.27*	0.04	0.16	0.22	*-0.19*	*-0.35*	0.06	0.05
R-2-16	0.11	*-0.13*	*-0.04*	0.20	0.22	0.21	*-0.40*	0.04	0.01
R-27-35	0.14	*-0.24*	*-0.09*	*-0.00*	*-0.30*	0.04	0.25	*-0.00*	*-0.09*

Appendix C.10. Continued. Foundation Germplasm: Relative selection index of 16 range standardized morphological traits related to agronomic potential in blue honeysuckle in 2012/2013 in the Fraser Valley, BC, Canada (n=18, J – Japanese, K – Kuril, R – Russian).

Genotype	Fruit Taste	Fruit Aroma	Fruit Mold	Fruit Flesh Firmness	Strength of Attachment	Stem Retention in Harvest	Picking Scar Quality	Total		
J-21-78	0.11	0.08	*-0.02*	*-0.11*	0.34	0.24	*-0.30*	0.03	Average	0.16
J-22-14	*-0.13*	0.13	0.03	0.03	0.20	0.18	0.10	0.80	Median	0.03
J-41-83	0.08	0.04	0.03	0.14	*-0.03*	*-0.31*	0.17	0.26	Minimum	*-0.91*
J-42-45	*-0.06*	*-0.06*	0.06	0.12	0.22	0.08	0.18	1.02	Maximum	1.02
J-43-87	*-0.03*	*-0.06*	0.06	0.13	0.29	0.15	0.15	0.97	Range	1.92
J-444-39	*-0.17*	*-0.25*	0.01	*-0.17*	*-0.20*	*-0.23*	0.10	*-0.91*		
J-45-14	0.17	0.20	0.06	*-0.01*	0.19	0.03	0.17	0.79		
J-46-55	0.08	0.15	0.03	*-0.06*	*-0.11*	0.06	*-0.36*	*-0.49*		
J-56-18	0.05	0.08	*-0.44*	*-0.16*	0.17	0.20	0.06	*-0.39*		
J-66-53	*-0.13*	*-0.17*	0.06	0.10	0.24	0.02	0.02	*-0.28*		
J-73-39	*-0.12*	*-0.09*	0.03	*-0.15*	*-0.25*	*-0.17*	0.12	*-0.02*		
K-3-03	0.10	*-0.06*	*-0.08*	0.00	*-0.02*	*-0.20*	*-0.01*	0.03	Average	0.01
K-3-05	0.11	*-0.07*	*-0.10*	0.00	*-0.07*	*-0.15*	0.00	*-0.05*	Median	*-0.04*
K-3-06	0.12	*-0.09*	*-0.16*	*-0.04*	*-0.03*	*-0.15*	0.00	*-0.04*	Minimum	*-0.09*
K-3-07	0.12	*-0.04*	*-0.10*	0.02	*-0.04*	*-0.12*	*-0.04*	0.20	Maximum	0.20
K-97-12	*-0.06*	0.10	*-0.10*	0.13	0.05	0.18	0.18	*-0.09*	Range	0.29
R-2-06	*-0.10*	*-0.02*	0.06	0.14	*-0.16*	*-0.14*	*-0.33*	*-0.51*	Average	0.12
R-2-07	0.22	0.01	0.06	0.11	0.06	0.13	*-0.01*	0.61	Median	0.29
R-2-10	*-0.02*	0.16	0.06	0.23	*-0.03*	0.10	*-0.04*	0.18	Minimum	*-1.42*
R-2-11	*-0.03*	0.05	0.06	0.06	*-0.13*	*-0.13*	0.16	0.40	Maximum	1.08
R-2-13	*-0.30*	-0.10	0.06	0.13	*-0.03*	0.03	0.15	0.81	Range	2.50
R-2-14	*-0.27*	0.00	0.06	0.07	0.16	0.10	0.09	*-0.20*		
R-2-16	0.13	0.26	0.06	0.17	*-0.03*	0.04	0.21	1.08		
R-27-35	0.10	*-0.01*	*-0.02*	*-0.30*	*-0.24*	*-0.13*	*-0.51*	*-1.42*		

Appendix C.11. Foundation and Improved Germplasm: Descriptive statistics of phenotypic averages for fruit morphological traits related to agronomic potential in blue honeysuckle in 2012/2013 in Chilliwack, BC, Canada.

		Japanese	Kuril	Russian	Japanese/ Kuril	Japanese/ Russian	Kuril/ Russian
Fruit Synanthy (1-2)	Average	1.35	1.16	1.15	1.22	1.33	1.23
	Median	1.29	1.00	1.00	1.15	1.29	1.20
	Minimum	1.11	1.00	1.00	1.00	1.00	1.00
	Maximum	1.88	1.57	1.75	2.00	2.00	2.00
	Range	0.76	0.57	0.75	1.00	1.00	1.00
Fruit Surface (1-5)	Average	2.14	1.69	3.00	1.84	2.23	2.24
	Median	1.89	1.71	3.00	1.85	2.11	2.29
	Minimum	1.11	1.29	2.00	1.00	1.00	1.00
	Maximum	3.44	2.00	4.75	3.25	4.25	4.14
	Range	2.33	0.71	2.75	2.25	3.25	3.14
Fruit Pubescence (1-9)	Average	1.67	3.20	1.91	2.56	1.92	2.06
	Median	1.25	2.56	1.00	2.43	1.71	1.50
	Minimum	1.00	1.67	1.00	1.00	1.00	1.00
	Maximum	3.00	6.71	3.57	4.75	5.22	6.33
	Range	2.00	5.05	2.57	3.75	4.22	5.33
Fruit Bloom (1-7)	Average	3.62	4.56	3.49	3.72	3.31	3.19
	Median	3.29	4.78	3.25	3.85	3.31	3.13
	Minimum	5.38	5.33	4.43	5.33	5.50	5.13
	Maximum	2.56	3.57	3.00	2.44	2.22	2.00
	Range	5.18	6.24	6.57	5.11	4.72	4.88
Fruit Colour (1-3)	Average	1.99	1.42	1.24	1.96	1.93	1.52
	Median	2.13	1.33	1.25	1.94	1.87	1.50
	Minimum	1.43	1.14	1.00	1.00	1.00	1.00
	Maximum	2.63	1.86	1.71	2.83	3.00	3.00
	Range	1.20	0.71	0.71	1.83	2.00	2.00

Appendix C.11. Continued. Foundation and Improved Germplasm: Phenotypic averages for fruit morphological traits related to agronomic potential in blue honeysuckle in 2012/2013 in Chilliwack, BC, Canada.

		Japanese	Kuril	Russian	Japanese/ Kuril	Japanese/ Russian	Kuril/ Russian
Fruit Shape in Cross-Section (1-5)	Average	2.23	3.74	2.84	2.56	2.53	3.37
	Median	2.33	4.00	2.71	2.44	2.63	3.44
	Minimum	3.00	4.33	3.75	3.67	4.00	5.00
	Maximum	1.63	2.71	2.25	1.00	1.00	1.00
	Range	4.63	4.38	4.50	3.33	3.00	2.00
Distal Opening Size (1-7)	Average	2.81	2.03	3.14	2.17	3.09	3.38
	Median	2.63	2.14	2.88	1.69	3.00	3.40
	Minimum	1.78	1.33	1.57	1.00	1.00	1.00
	Maximum	3.67	2.67	5.50	4.75	6.25	7.00
	Range	1.89	1.33	3.93	3.75	5.25	6.00
Heterogeneity of Fruit Size (1-5)	Average	3.09	2.89	2.97	3.18	3.12	3.09
	Median	3.00	2.81	3.03	3.15	3.07	3.09
	Minimum	2.59	2.50	2.50	2.67	2.23	1.20
	Maximum	3.73	3.50	3.24	3.91	4.00	4.00
	Range	1.15	1.00	0.74	1.24	1.77	2.80
Heterogeneity of Fruit Shape (1-5)	Average	3.09	2.81	3.39	3.04	3.26	3.15
	Median	3.06	2.71	3.24	3.00	3.21	3.19
	Minimum	2.53	2.53	2.50	2.44	2.56	2.00
	Maximum	3.78	3.44	5.00	3.73	4.00	3.93
	Range	1.25	0.90	2.50	1.28	1.44	1.93

Appendix C.11. Continued. Foundation and Improved Germplasm: Phenotypic averages for fruit morphological traits related to agronomic potential in blue honeysuckle in 2012/2013 in Chilliwack, BC, Canada.

		Japanese	Kuril	Russian	Japanese/ Kuril	Japanese/ Russian	Kuril/ Russian
Fruit Taste (1-6)	Average	2.67	2.67	3.12	2.80	2.81	3.07
	Median	2.67	2.53	3.28	2.66	2.71	3.00
	Minimum	1.94	2.33	2.00	2.00	1.69	1.89
	Maximum	3.39	3.47	4.00	4.24	4.25	4.44
	Range	1.45	1.13	2.00	2.24	2.56	2.55
Fruit Aroma (1-7)	Average	3.84	3.57	4.09	3.65	3.67	3.96
	Median	4.14	3.40	4.32	3.70	3.68	4.00
	Minimum	5.06	4.07	5.17	5.06	5.31	7.00
	Maximum	1.69	3.33	2.67	2.00	2.31	2.67
	Range	4.63	7.27	5.50	4.94	5.00	3.67
Fruit Mold (1-4)	Average	1.35	1.84	1.11	1.29	1.32	1.18
	Median	1.11	1.78	1.00	1.11	1.11	1.11
	Minimum	1.00	1.33	1.00	1.00	1.00	1.00
	Maximum	3.78	2.33	1.89	2.40	3.00	2.11
	Range	2.78	1.00	0.89	1.40	2.00	1.11
Fruit Flesh Firmness (1-7)	Average	3.37	3.30	2.94	3.35	3.98	3.90
	Median	3.50	3.53	2.50	3.37	3.87	3.96
	Minimum	2.50	2.40	1.50	1.29	1.93	1.00
	Maximum	4.33	3.93	5.08	5.31	6.00	6.20
	Range	1.83	1.53	3.58	4.02	4.07	5.20

Appendix C.11. Continued. Foundation and Improved Germplasm: Phenotypic averages for fruit morphological traits related to agronomic potential in blue honeysuckle in 2012/2013 in Chilliwack, BC, Canada.

		Japanese	Kuril	Russian	Japanese/ Kuril	Japanese/ Russian	Kuril/ Russian
Strength of Fruit Attachment (1-9)	Average	4.54	5.17	4.13	4.06	4.53	5.02
	Median	4.00	5.18	3.64	4.00	4.44	5.03
	Minimum	2.28	4.73	3.17	1.65	2.35	2.09
	Maximum	6.41	5.75	7.56	6.31	7.56	6.94
	Range	4.13	1.02	4.40	4.67	5.21	4.85
Stems Retaining in Harvest (1-7)	Average	2.00	3.27	3.42	2.05	2.30	2.73
	Median	1.65	3.47	3.08	2.00	2.00	2.65
	Minimum	1.11	2.38	2.41	1.00	1.00	1.00
	Maximum	3.94	3.94	5.22	3.56	5.25	4.69
	Range	2.83	1.56	2.81	2.56	4.25	3.69
Picking Scar Quality (1-4)	Average	1.77	1.70	1.92	1.66	1.76	1.96
	Median	1.67	1.81	1.76	1.39	1.57	1.78
	Minimum	1.00	1.06	1.00	1.00	1.00	1.00
	Maximum	3.41	1.94	3.25	3.33	3.25	3.67
	Range	2.41	0.88	2.25	2.33	2.25	2.67

Appendix C.12. Improved Germplasm: Relative[1] selection index of 16 range standardized fruit morphological traits related to agronomic potential in blue honeysuckle in 2012/2013 in the Chilliwack, BC, Canada (n=6).

Trait Averages			
	Japanese/Kuril	Japanese/Russian	Kuril/Russian
Fruit Synanthy	0.02	*-0.03*	0.02
Fruit Surface	0.07	*-0.01*	*-0.01*
Fruit Pubescence	*-0.05*	0.02	0.01
Fruit Bloom	*-0.05*	0.01	0.03
Fruit Colour	*-0.07*	*-0.06*	0.07
Fruit Shape in Cross-Section	0.06	0.07	*-0.10*
Distal Opening Size	0.12	*-0.01*	*-0.05*
Heterogeneity of Fruit Size	*-0.02*	0.00	0.00
Heterogeneity of Fruit Shape	0.02	*-0.02*	0.00
Fruit Taste	0.01	0.01	*-0.02*
Fruit Aroma	0.02	0.02	*-0.02*
Fruit Mold	0.00	*-0.01*	0.02
Fruit Flesh Firmness	0.06	*-0.03*	*-0.02*
Strength of Attachment	0.06	0.01	*-0.04*
Stems Retained in Harvest	0.06	0.02	*-0.04*
Picking Scar Quality	0.04	0.01	*-0.04*
Phenotypic Selection Index Scores			
Average	0.36	*-0.01*	*-0.20*
Median	0.50	0.04	*-0.18*
Minimum	*-1.57*	*-1.84*	*-2.44*
Maximum	1.73	1.02	1.93
Range	3.30	2.87	4.37

[1]Negative numbers in italics, the lower the number the worse the rating.

9.4 Appendix D

Appendix D.1. Foundation Germplasm: Phenotypic average[1] +/- SE and rankings for fruit quality traits in blue honeysuckle and comparison crops in 2012/2013 in the Fraser Valley, BC, Canada (n=18, J – Japanese, K – Kuril, R – Russian).

Genotype	Dry Matter (%)	Total Soluble Solids (%)
J-21-78	16.2 ± 0.2 k-m (12,2)	12.84 ± 0.24 pq (3,2)
J-22-14	14.5 ± 0.2 d-g (29,12)	11.11 ± 0.15 j-n (17,7)
J-41-83	15.4 ± 0.2 g-l (16,4)	11.50 ± 0.16 mn (8,5)
J-42-45	15.0 ± 0.3 f-j (21,8)	10.97 ± 0.17 i-m (19,8)
J-43-87	14.6 ± 0.2 c-g (27,11)	10.63 ± 0.18 f-k (22,10)
J-444-39	14.8 ± 0.3 d-h (25,10)	9.93 ± 0.34 e (32,12)
J-45-14	15.1 ± 0.4 f-j (20,7)	11.83 ± 0.35 no (7,4)
J-46-55	15.9 ± 0.3 j-l (13,3)	12.77 ± 0.36 pq (4,3)
J-56-18	15.2 ± 0.3 g-k (17,5)	11.40 ± 0.35 l-n (11,6)
J-66-53	16.9 ± 0.5 mn (8,1)	12.95 ± 0.17 pq (2,1)
J-73-39	14.9 ± 0.4 e-i (24,9)	10.21 ± 0.27 e-h (27,11)
K-3-03	14.0 ± 0.3 c-e (30,3)	10.29 ± 0.28 e-i (26,3)
K-3-05	13.7 ± 0.2 cd (34,5)	10.05 ± 0.27 ef (31,5)
K-3-06	14.0 ± 0.3 c-e (31,4)	10.51 ± 0.18 e-j (24,2)
K-3-07	14.5 ± 0.4 c-g (28,2)	10.12 ± 0.19 e-h (30,4)
K-97-12	14.7 ± 0.5 d-j (26,1)	10.82 ± 0.32 g-m (20,1)
R-2-06	13.8 ± 0.3 b-f (32,8)	9.70 ± 0.41 d-g (34,9)
R-2-07	15.0 ± 0.3 f-l (22,6)	11.00 ± 0.24 j-n (18,4)
R-2-10	15.1 ± 0.1 f-l (19,5)	10.62 ± 0.36 e-m (23,5)
R-2-11	13.8 ± 0.3 c-f (33,9)	10.34 ± 0.36 e-l (25,6)
R-2-13	16.5 ± 2.0 h-p (10,3)	9.70 ± NA (33,8)
R-2-14	13.1 ± 0.4 bc (35,10)	8.68 ± 0.48 cd (36,11)
R-2-16	18.2 ± 0.5 pq (3,1)	11.17 ± 0.17 j-n (16,3)
R-27-35	15.8 ± 0.3 i-l (14,4)	11.43 ± 0.26 mn (9,2)

[1]Genotypes not connected by the same letter are statistically different ($p < 0.05$) based on linear contrasts extracted from linear mixed models. In brackets, overall rank followed by group rank (J-PP ranked with Japanese and U of S cultivars ranked with Russian group).

Appendix D.1. Continued. Foundation Germplasm: Phenotypic average[1] +/- SE and rankings for fruit quality traits in blue honeysuckle and comparison crops in 2012/2013 in the Fraser Valley, BC, Canada (n=18, J – Japanese, K – Kuril, R – Russian).

Genotype	Dry Matter (%)	Total Soluble Solids (%)
J-PP	15.1 ± 0.2 g-l (18,6)	10.75 ± 0.25 h-m (21,9)
'Borealis'	12.6 ± 0.3 b (36,11)	8.72 ± 0.27 d (35,10)
'Tundra'	14.9 ± 0.3 f-j (23,7)	10.19 ± 0.23 e-j (29,7)
'Indigo Gem'	17.0 ± 0.4 no (7,2)	12.44 ± 0.38 op (6,1)
Blueberry		
'Bluecrop'	18.0 ± 0.5 o-q (4,2)	12.67 ± 0.42 pq (5,2)
'Duke'	16.9 ± 0.6 mn (9,3)	11.19 ± 0.36 k-n (15,4)
'Elliott'	20.4 ± 0.9 r (1,1)	13.37 ± 0.43 q (1,1)
'Reka'	16.2 ± 0.5 lm (11,4)	11.38 ± 0.34 l-n (13,3)
Raspberry		
'Cascade Bounty'	15.5 ± 0.2 h-l (15,4)	10.20 ± 0.26 e-h (28,4)
'Chemainus'	17.1 ± 0.3 no (6,3)	11.28 ± 0.25 k-n (14,3)
'Meeker'	18.5 ± 0.2 q (2,1)	11.39 ± 0.31 mn (12,2)
'Saanich'	17.8 ± 0.4 n-q (5,2)	11.42 ± 0.31 mn (10,1)
Strawberry		
'Puget Reliance'	9.8 ± 0.4 a (39,3)	7.42 ± 0.27 ab (38,2)
'Rainier'	9.6 ± 0.1 a (40,4)	6.95 ± 0.14 a (40,4)
'Stolo'	10.0 ± 0.3 a (37,1)	7.16 ± 0.16 ab (39,3)
'Totem'	10.0 ± 0.3 a (38,2)	7.71 ± 0.28 bc (37,1)

[1]Genotypes not connected by the same letter are statistically different ($p < 0.05$) based on linear contrasts extracted from linear mixed models. In brackets, overall rank followed by group rank (J-PP ranked with Japanese and U of S cultivars ranked with Russian group).

Appendix D.2. Foundation Germplasm: Phenotypic average[1] +/- SE and rankings for fruit quality traits in blue honeysuckle and comparison crops in 2012/2013 in the Fraser Valley, BC, Canada (n=18, J – Japanese, K – Kuril, R – Russian, CAE – citric acid equivalents, TSS – total soluble solids, TA – titratable acidity).

Genotype	Titratable Acidity (% CAE)	pH	TSS:TA
J-21-78	2.37 ± 0.04 mn (12,9)	2.98 ± 0.02 g-j (19,4)	5.46 ± 0.17 d-f (18,3)
J-22-14	3.32 ± 0.07 r (2,2)	2.84 ± 0.04 ab (39,11)	3.37 ± 0.09 ab (38,11)
J-41-83	2.67 ± 0.03 op (9,7)	2.93 ± 0.02 d-g (28,6)	4.32 ± 0.08 a-e (30,6)
J-42-45	2.74 ± 0.04 p (6,4)	2.85 ± 0.02 bc (37,9)	4.02 ± 0.09 a-d (34,8)
J-43-87	2.68 ± 0.05 op (8,6)	2.85 ± 0.03 bc (38,10)	3.99 ± 0.09 a-d (36,10)
J-444-39	3.58 ± 0.09 s (1,1)	2.78 ± 0.03 a (40,12)	2.78 ± 0.09 a (40,12)
J-45-14	2.05 ± 0.03 h-k (24,11)	2.99 ± 0.01 g-j (16,2)	5.79 ± 0.22 ef (16,2)
J-46-55	1.76 ± 0.12 fg (28,12)	3.00 ± 0.03 h-k (15,1)	7.66 ± 0.49 gh (10,1)
J-56-18	2.76 ± 0.06 pq (5,3)	2.88 ± 0.01 b-e (35,8)	4.17 ± 0.18 a-e (33,7)
J-66-53	2.70 ± 0.04 op (7,5)	2.93 ± 0.01 e-g (26,5)	4.82 ± 0.11 b-e (26,5)
J-73-39	2.56 ± 0.04 o (11,8)	2.91 ± 0.01 c-g (30,7)	4.00 ± 0.12 a-d (35,9)
K-3-03	2.21 ± 0.03 lm (14,2)	2.94 ± 0.02 e-h (23,3)	4.66 ± 0.13 a-e (28,3)
K-3-05	2.20 ± 0.04 kl (15,3)	2.95 ± 0.02 f-h (21,2)	4.58 ± 0.11 a-e (29,4)
K-3-06	2.15 ± 0.03 j-l (17,4)	2.93 ± 0.03 e-g (27,4)	4.90 ± 0.13 b-e (23,1)
K-3-07	2.12 ± 0.04 h-l (20,5)	2.91 ± 0.03 b-f (32,5)	4.79 ± 0.11 b-e (27,2)
K-97-12	2.64 ± 0.12 op (10,1)	2.96 ± 0.02 f-h (20,1)	4.23 ± 0.27 a-e (31,5)
R-2-06	1.95 ± 0.15 g-j (27,9)	2.95 ± 0.05 c-j (22,7)	5.05 ± 0.40 a-g (20,5)
R-2-07	1.65 ± 0.05 ef (29,10)	3.19 ± 0.04 no (6,1)	6.74 ± 0.29 f-h (13,2)
R-2-10	2.15 ± 0.1 h-l (18,5)	2.94 ± 0.03 c-h (25,9)	4.97 ± 0.14 b-g (21,6)
R-2-11	2.19 ± 0.11 i-m (16,4)	2.99 ± 0.05 f-j (17,6)	4.82 ± 0.38 a-f (25,8)
R-2-13	2.86 ± NA (4,2)	2.91 ± NA (31,11)	3.39 ± NA (37,10)
R-2-14	2.10 ± 0.13 h-l (22,6)	2.94 ± 0.03 b-i (24,8)	4.20 ± 0.38 a-f (32,9)
R-2-16	1.64 ± 0.11 ef (30,11)	3.08 ± 0.04 k-n (11,3)	6.99 ± 0.50 f-h (12,1)
R-27-35	1.98 ± 0.03 hi (25,8)	3.05 ± 0.04 i-l (14,5)	5.79 ± 0.17 ef (15,3)

[1]Genotypes not connected by the same letter are statistically different (p < 0.05) based on linear contrasts extracted from linear mixed models. In brackets, overall rank followed by group rank (J-PP ranked with Japanese and U of S cultivars ranked with Russian group).

Appendix D.2. Continued. Foundation Germplasm: Phenotypic average[1] +/- SE and rankings for fruit quality traits in blue honeysuckle and comparison crops in 2012/2013 in the Fraser Valley, BC, Canada (n=18, J – Japanese, K – Kuril, R – Russian, CAE – citric acid equivalents, TSS – total soluble solids, TA – titratable acidity).

Genotype	Titratable Acidity (% CAE)	pH	TSS:TA
J-PP	2.11 ± 0.05 h-l (21,10)	2.99 ± 0.03 g-i (18,3)	5.10 ± 0.10 c-f (19,4)
'Borealis'	2.95 ± 0.06 q (3,1)	2.92 ± 0.03 b-g (29,10)	2.96 ± 0.08 a-c (39,11)
'Tundra'	2.08 ± 0.07 h-l (23,7)	3.07 ± 0.03 j-m (12,4)	4.93 ± 0.13 b-f (22,7)
'Indigo Gem'	2.26 ± 0.05 lm (13,3)	3.09 ± 0.03 lm (10,2)	5.54 ± 0.22 e-g (17,4)
Blueberry			
'Bluecrop'	0.81 ± 0.08 bc (35,3)	3.11 ± 0.04 l-n (9,2)	18.33 ± 2.16 m (1,1)
'Duke'	0.92 ± 0.11 c (34,2)	3.06 ± 0.06 j-l (13,3)	14.57 ± 1.91 l (3,3)
'Elliott'	1.22 ± 0.12 d (33,1)	2.89 ± 0.04 b-e (34,4)	12.82 ± 1.66 k (4,4)
'Reka'	0.77 ± 0.07 a-c (36,4)	3.13 ± 0.03 m-o (7,1)	17.43 ± 2.02 m (2,2)
Raspberry			
'Cascade Bounty'	2.12 ± 0.04 i-l (19,1)	2.86 ± 0.02 b-d (36,4)	4.85 ± 0.18 b-e (24,4)
'Chemainus'	1.96 ± 0.06 h (26,2)	2.89 ± 0.02 b-f (33,3)	5.84 ± 0.22 ef (14,3)
'Meeker'	1.56 ± 0.07 e (31,3)	3.11 ± 0.02 l-n (8,2)	7.65 ± 0.51 gh (11,2)
'Saanich'	1.28 ± 0.05 d (32,4)	3.20 ± 0.02 o (5,1)	9.12 ± 0.45 hi (9,1)
Strawberry			
'Puget Reliance'	0.69 ± 0.02 ab (38,2)	3.43 ± 0.03 p (4,4)	10.83 ± 0.48 ij (7,3)
'Rainier'	0.63 ± 0.02 a (40,4)	3.47 ± 0.03 p (3,3)	11.19 ± 0.43 jk (6,2)
'Stolo'	0.64 ± 0.02 a (39,3)	3.49 ± 0.02 p (1,1)	11.39 ± 0.41 jk (5,1)
'Totem'	0.74 ± 0.01 ab (37,1)	3.47 ± 0.03 p (2,2)	10.45 ± 0.35 ij (8,4)

[1]Genotypes not connected by the same letter are statistically different (p < 0.05) based on linear contrasts extracted from linear mixed models. In brackets, overall rank followed by group rank (J-PP ranked with Japanese and U of S cultivars ranked with Russian group).

Appendix D.3. Foundation Germplasm: Phenotypic averages for additional assay durations for biochemical determinations of antioxidant activity in foundation blue honeysuckle groups and comparison crops in 2012/2013 in the Fraser Valley, BC, Canada (FW – fresh weight, DW – dry weight, TE – Trolox equivalents, AAE – ascorbic acid equivalents).

		mmol TE/100 g FW at 15 min						mmol TE/100 g DW at 15 min					
		Japanese	Kuril	Russian	Blueberry	Raspberry	Strawberry	Japanese	Kuril	Russian	Blueberry	Raspberry	Strawberry
Total Antioxidant Capacity	Average	2.3	2.7	2.6	2.4	2.6	1.4	14.8	19.2	16.9	13.6	16.4	14.2
	Median	2.3	2.7	2.4	2.3	2.7	1.3	15.0	19.6	16.9	13.5	16.5	13.9
	Minimum	1.5	2.5	2.3	1.8	2.1	1.2	9.2	18.0	16.0	11.1	14.9	12.3
	Maximum	2.8	2.9	3.3	3.2	2.9	1.6	18.4	20.0	17.9	16.0	17.5	16.6
	Range	1.3	0.4	1.0	1.3	0.7	0.5	9.2	2.0	1.9	4.9	2.6	4.2

		mmol AAE/100 g FW at 14 min						mmol AAE/100 g DW at 14 min					
		Japanese	Kuril	Russian	Blueberry	Raspberry	Strawberry	Japanese	Kuril	Russian	Blueberry	Raspberry	Strawberry
Ferric Reducing Antioxidant Potential	Average	6.7	7.4	8.0	6.8	6.3	3.3	43.6	52.3	52.4	38.2	39.4	34.2
	Median	6.4	7.2	7.6	6.2	6.2	3.3	42.8	51.0	52.8	36.3	39.7	34.5
	Minimum	5.9	6.9	6.7	5.5	5.5	3.2	36.1	49.2	43.8	33.9	33.2	32.1
	Maximum	8.5	8.6	10.5	9.1	7.2	3.5	55.7	58.4	59.6	46.1	45.1	35.8
	Range	2.6	1.7	3.8	3.6	1.7	0.3	19.5	9.2	15.8	12.2	11.9	3.6

Appendix D.4. Foundation Germplasm: Phenotypic average[1] +/- SE and rankings for fresh weight calculations of nutritional content in blue honeysuckle and comparison crops in 2012/2013 in the Fraser Valley, BC, Canada (n=18, J – Japanese, K – Kuril, R – Russian, FW – fresh weight, GAE – gallic acid equivalents, TE – Trolox equivalents, AAE – ascorbic acid equivalents).

Genotype	Total Phenolics (mg GAE/100 g FW)	Trolox Antioxidant Capacity (mmol TE/100 g FW) at 5 min	Ferric Reducing Antioxidant Potential (mmol AAE/100 g FW) at 4 min
J-21-78	410.5 ± 12.6 d-g (30,8)	1.90 ± 1.90 fg (28,6)	4.82 ± 0.29 c-f (29,7)
J-22-14	364.8 ± 6.4 a-d (36,12)	2.03 ± 2.03 f-i (25,5)	5.28 ± 0.16 e-j (22,5)
J-41-83	372.9 ± 21.9 a-d (35,11)	1.76 ± 1.76 d-f (32,10)	4.70 ± 0.16 c-e (31,9)
J-42-45	416.2 ± 29 d-h (29,7)	1.86 ± 1.86 fg (30,8)	5.40 ± 0.30 f-k (21,4)
J-43-87	568.9 ± 30.5 m-q (9,1)	2.16 ± 2.16 g-j (22,2)	5.85 ± 0.23 j-n (17,2)
J-444-39	494.2 ± 59.0 h-m (18,4)	2.16 ± 2.16 g-j (23,3)	5.59 ± 0.34 g-l (19,3)
J-45-14	468.7 ± 21.5 f-j (24,5)	1.48 ± 1.48 c-e (34,11)	4.57 ± 0.09 cd (33,11)
J-46-55	387.1 ± 9.2 b-e (33,9)	2.08 ± 2.08 f-i (24,4)	4.60 ± 0.18 cd (32,10)
J-56-18	555.8 ± 22.7 l-p (13,2)	2.63 ± 2.63 k-m (6,1)	6.25 ± 0.33 m-o (14,1)
J-66-53	461.6 ± 23.5 f-j (26,6)	1.28 ± 1.28 bc (37,12)	4.54 ± 0.26 cd (34,12)
J-73-39	377.9 ± 17.9 b-d (34,10)	1.83 ± 1.83 fg (31,9)	4.78 ± 0.20 c-f (30,8)
K-3-03	523.6 ± 26.5 j-o (14,2)	2.35 ± 2.35 jk (20,5)	5.55 ± 0.24 h-l (20,5)
K-3-05	478.3 ± 29.8 g-k (19,3)	2.50 ± 2.50 kl (11,3)	6.14 ± 0.23 l-n (15,4)
K-3-06	455.8 ± 19.9 e-i (27,5)	2.63 ± 2.63 k-m (5,2)	6.30 ± 0.19 m-o (13,3)
K-3-07	557.3 ± 24.5 m-p (12,1)	2.45 ± 2.45 kl (15,4)	6.45 ± 0.29 n-q (11,2)
K-97-12	470.0 ± 43.9 f-l (23,4)	2.91 ± 2.91 m (2,1)	7.59 ± 0.60 st (4,1)
R-2-06	655.2 ± 48.6 p-r (3,3)	2.44 ± 2.44 i-m (16,7)	7.30 ± 0.25 q-s (6,5)
R-2-07	599.7 ± 23.8 o-q (6,5)	2.39 ± 2.39 kl (17,8)	6.45 ± 0.19 n-r (12,9)
R-2-10	631.2 ± 11.5 pq (5,4)	2.53 ± 2.53 k-m (9,3)	7.31 ± 0.18 rs (5,4)
R-2-11	563.5 ± 22.8 k-q (11,7)	2.20 ± 2.20 h-k (21,11)	6.12 ± 0.31 k-p (16,10)
R-2-13	816.0 ± 180.6 rs (1,1)	2.78 ± 2.78 k-m (3,2)	8.75 ± 1.63 tu (2,2)
R-2-14	566.5 ± 27.7 i-q (10,6)	2.37 ± 2.37 h-l (18,9)	6.77 ± 0.36 m-s (10,8)

[1]Genotypes not connected by the same letter are statistically different (p < 0.05) based on linear contrasts extracted from linear mixed models. In brackets, overall rank followed by group rank (J-PP ranked with Japanese and U of S cultivars ranked with Russian group).

Appendix D.4. Continued. Foundation Germplasm: Phenotypic average[1] +/- SE and rankings for fresh weight calculations of nutritional content in blue honeysuckle and comparison crops in 2012/2013 in the Fraser Valley, BC, Canada (n=18, J – Japanese, K – Kuril, R – Russian, FW – fresh weight, GAE – gallic acid equivalents, TE – Trolox equivalents, AAE – ascorbic acid equivalents).

Genotype	Total Phenolics (mg GAE/100 g FW)	Trolox Antioxidant Capacity (mmol TE/100 g FW) at 5 min	Ferric Reducing Antioxidant Potential (mmol AAE/100 g FW) at 4 min
R-2-16	815.2 ± 26.0 s (2,2)	3.51 ± 3.51 n (1,1)	9.10 ± 0.40 u (1,1)
R-27-35	501.8 ± 27.5 i-n (17,9)	2.46 ± 2.46 kl (13,6)	5.73 ± 0.10 i-m (18,11)
J-PP	521.2 ± 38.7 i-o (15,3)	1.86 ± 1.86 f-h (29,7)	4.94 ± 0.16 d-h (27,6)
'Borealis'	477.9 ± 84.0 f-k (20,10)	2.36 ± 2.36 i-l (19,10)	6.89 ± 0.23 o-s (9,7)
'Tundra'	477.2 ± 56.0 f-l (21,11)	2.52 ± 2.52 k-m (10,4)	8.66 ± 0.35 u (3,3)
'Indigo Gem'	502.2 ± 29.4 i-n (16,8)	2.48 ± 2.48 k-m (12,5)	6.96 ± 0.49 p-s (8,6)
Blueberry			
'Bluecrop'	462.0 ± 20.1 f-j (25,2)	1.75 ± 1.75 ef (33,3)	4.98 ± 0.24 d-h (25,3)
'Duke'	451.0 ± 24.2 e-j (28,3)	1.92 ± 1.92 f-h (27,2)	5.12 ± 0.26 d-i (23,2)
'Elliott'	588.2 ± 42.9 o-q (7,1)	2.57 ± 2.57 k-m (7,1)	7.00 ± 0.52 q-s (7,1)
'Reka'	406.7 ± 21.1 c-g (31,4)	1.43 ± 1.43 cd (35,4)	4.33 ± 0.20 bc (35,4)
Raspberry			
'Cascade Bounty'	405.1 ± 25.1 d-f (32,4)	1.97 ± 1.97 f-h (26,4)	3.81 ± 0.27 b (36,4)
'Chemainus'	470.3 ± 22.8 f-j (22,3)	2.56 ± 2.56 kl (8,2)	4.96 ± 0.16 d-g (26,2)
'Meeker'	571.6 ± 29.5 n-q (8,2)	2.67 ± 2.67 lm (4,1)	5.03 ± 0.15 d-h (24,1)
'Saanich'	632.0 ± 20.6 q (4,1)	2.45 ± 2.45 kl (14,3)	4.86 ± 0.17 c-f (28,3)
Strawberry			
'Puget Reliance'	303.8 ± 11.8 a (39,3)	1.03 ± 1.03 ab (39,3)	2.50 ± 0.09 a (38,2)
'Rainier'	301.6 ± 13.8 a (40,4)	0.98 ± 0.98 a (40,4)	2.45 ± 0.06 a (39,3)
'Stolo'	324.8 ± 4.1 ab (38,2)	1.22 ± 1.22 a-c (38,2)	2.35 ± 0.06 a (40,4)
'Totem'	335.0 ± 12.4 a-c (37,1)	1.40 ± 1.40 c (36,1)	2.63 ± 0.11 a (37,1)

[1]Genotypes not connected by the same letter are statistically different (p < 0.05) based on linear contrasts extracted from linear mixed models. In brackets, overall rank followed by group rank (J-PP ranked with Japanese and U of S cultivars ranked with Russian group).

Appendix D.5. Foundation Germplasm: Phenotypic average[1] +/- SE and rankings for dry weight calculations of nutritional content in blue honeysuckle and comparison crops in 2012/2013 in the Fraser Valley, BC, Canada (n=18, J – Japanese, K – Kuril, R – Russian, DW – dry weight, GAE – gallic acid equivalents, TE – Trolox equivalents, AAE – ascorbic acid equivalents).

Genotype	Total Phenolics (mg GAE/100 g DW)	Trolox Antioxidant Capacity (mmol TE/100 g DW) at 5 min	Ferric Reducing Antioxidant Potential (mmol AAE/100 g DW) at 4 min
J-21-78	2545.6 ± 80.5 ab (35,8)	11.77 ± 0.34 ef (32,9)	29.67 ± 1.59 e-i (29,10)
J-22-14	2525.9 ± 42.7 a (37,10)	14.03 ± 0.85 g-n (24,4)	36.51 ± 1.02 k (20,4)
J-41-83	2425.2 ± 136.1 a (40,12)	11.42 ± 0.61 c-f (34,10)	30.55 ± 0.93 f-i (27,8)
J-42-45	2750.2 ± 152.2 a-c (32,7)	12.28 ± 0.54 e-g (29,6)	35.69 ± 1.33 k (21,5)
J-43-87	3888.3 ± 169.5 k-m (8,1)	14.78 ± 1.01 k-p (21,2)	40.03 ± 1.10 l-n (16,2)
J-444-39	3308.8 ± 353.5 d-i (16,4)	14.53 ± 0.59 i-p (22,3)	37.59 ± 1.69 kl (18,3)
J-45-14	3097.2 ± 109.4 c-f (28,5)	9.81 ± 0.61 b-d (37,11)	30.32 ± 0.40 e-i (28,9)
J-46-55	2431.5 ± 24.2 a (39,11)	13.01 ± 0.79 f-k (26,5)	29.00 ± 1.18 b-g (31,11)
J-56-18	3635.6 ± 112.1 h-k (11,2)	17.17 ± 0.48 s-u (8,1)	40.93 ± 1.79 l-n (15,1)
J-66-53	2750.6 ± 145.4 a-c (31,6)	7.79 ± 0.77 a (40,12)	27.04 ± 1.51 b-e (35,12)
J-73-39	2532.8 ± 84.4 ab (36,9)	12.26 ± 0.72 e-h (30,7)	32.08 ± 0.99 h-j (24,7)
K-3-03	3731.2 ± 160.2 i-l (10,2)	16.69 ± 0.64 q-t (11,5)	39.45 ± 1.27 lm (17,5)
K-3-05	3496.6 ± 221.3 f-j (13,3)	18.11 ± 0.74 t-w (5,3)	44.55 ± 1.04 op (11,4)
K-3-06	3286.4 ± 167.4 d-h (18,4)	18.69 ± 0.74 u-w (3,2)	45.05 ± 1.01 op (9,2)
K-3-07	3859.4 ± 124.2 j-l (9,1)	16.95 ± 0.56 r-u (9,4)	44.66 ± 1.34 op (10,3)
K-97-12	3178.2 ± 256.9 c-h (25,5)	19.66 ± 1.36 w (1,1)	51.39 ± 3.66 q (5,1)
R-2-06	4723.1 ± 283.1 n (2,2)	17.57 ± 0.77 q-w (6,3)	52.72 ± 1.08 q (2,2)
R-2-07	4005.4 ± 130.7 j-m (7,7)	15.97 ± 0.33 p-t (14,8)	43.17 ± 1.23 m-o (14,10)
R-2-10	4165.0 ± 77.9 k-n (5,5)	16.67 ± 0.35 q-v (12,6)	48.24 ± 1.20 pq (8,7)
R-2-11	4077.8 ± 114.7 k-n (6,6)	15.94 ± 0.64 m-t (15,9)	44.43 ± 2.34 n-p (12,8)
R-2-13	4879.3 ± 503.9 n (1,1)	16.83 ± 0.04 l-w (10,5)	52.58 ± 3.49 q (3,3)
R-2-14	4330.7 ± 185.0 l-n (4,4)	18.18 ± 1.00 r-w (4,2)	51.78 ± 2.40 q (4,4)

[1]Genotypes not connected by the same letter are statistically different (p < 0.05) based on linear contrasts extracted from linear mixed models. In brackets, overall rank followed by group rank (J-PP ranked with Japanese and U of S cultivars ranked with Russian group).

Appendix D.5. Continued. Foundation Germplasm: Phenotypic average[1] +/- SE and rankings for dry weight calculations of nutritional content in blue honeysuckle and comparison crops in 2012/2013 in the Fraser Valley, BC, Canada (n=18, J – Japanese, K – Kuril, R – Russian, DW – dry weight, GAE – gallic acid equivalents, TE – Trolox equivalents, AAE – ascorbic acid equivalents).

Genotype	Total Phenolics (mg GAE/100 g DW)	Trolox Antioxidant Capacity (mmol TE/100 g DW) at 5 min	Ferric Reducing Antioxidant Potential (mmol AAE/100 g DW) at 4 min
R-2-16	4461.4 ± 116.2 mn (3,3)	19.15 ± 0.37 vw (2,1)	49.61 ± 1.49 q (6,5)
R-27-35	3207.3 ± 185.9 d-g (23,10)	15.55 ± 0.65 m-s (18,11)	36.54 ± 0.88 k (19,11)
J-PP	3435.7 ± 244.3 e-i (14,3)	12.25 ± 0.54 f-j (31,8)	32.57 ± 0.83 ij (23,6)
'Borealis'	3151.4 ± 388.6 c-f (26,11)	16.26 ± 0.64 p-t (13,7)	48.97 ± 1.57 q (7,6)
'Tundra'	3281.1 ± 374.0 d-h (19,8)	17.34 ± 0.27 s-w (7,4)	59.48 ± 1.65 r (1,1)
'Indigo Gem'	3258.1 ± 238.0 d-h (21,9)	15.68 ± 0.28 n-s (17,10)	43.67 ± 1.71 no (13,9)
Blueberry			
'Bluecrop'	2578.8 ± 69.3 ab (34,3)	9.57 ± 0.86 a-c (38,3)	27.72 ± 0.73 b-f (34,3)
'Duke'	2724.8 ± 58.6 a-c (33,2)	11.57 ± 0.61 d-f (33,2)	31.03 ± 0.67 g-i (25,2)
'Elliott'	2970.7 ± 98.5 b-e (29,1)	13.00 ± 0.89 f-l (27,1)	35.26 ± 1.22 jk (22,1)
'Reka'	2503.1 ± 75.4 a (38,4)	8.65 ± 0.64 ab (39,4)	26.62 ± 0.64 a-d (36,4)
Raspberry			
'Cascade Bounty'	3139.9 ± 94.0 c-f (27,3)	15.07 ± 0.51 m-q (20,3)	29.14 ± 0.98 d-h (30,2)
'Chemainus'	2919.1 ± 116.7 b-d (30,4)	15.91 ± 0.49 o-s (16,1)	30.87 ± 0.85 g-i (26,1)
'Meeker'	3259.3 ± 144.1 d-h (20,2)	15.41 ± 0.56 m-r (19,2)	28.97 ± 1.05 c-g (32,3)
'Saanich'	3606.7 ± 74.8 g-k (12,1)	13.99 ± 0.60 h-m (25,4)	27.75 ± 0.72 b-f (33,4)
Strawberry			
'Puget Reliance'	3223.0 ± 179.3 d-g (22,3)	11.23 ± 1.28 c-f (35,3)	26.11 ± 0.89 ab (38,2)
'Rainier'	3189.0 ± 154.4 d-f (24,4)	10.42 ± 1.18 c-e (36,4)	25.92 ± 0.69 ab (39,3)
'Stolo'	3308.6 ± 98.0 e-h (17,2)	12.44 ± 0.60 f-i (28,2)	23.74 ± 0.42 a (40,4)
'Totem'	3371.3 ± 94.7 e-i (15,1)	14.22 ± 0.40 j-o (23,1)	26.29 ± 0.63 a-c (37,1)

[1]Genotypes not connected by the same letter are statistically different (p < 0.05) based on linear contrasts extracted from linear mixed models. In brackets, overall rank followed by group rank (J-PP ranked with Japanese and U of S cultivars ranked with Russian group).

Appendix D.6. Foundation Germplasm: Phenotypic average[1] +/- SE and rankings for Trolox antioxidant capacity assay at 15 min assay duration in blue honeysuckle and comparison crops in 2012/2013 in the Fraser Valley, BC, Canada (n=18, J – Japanese, K – Kuril, R – Russian, FW – fresh weight, DW – dry weight, TE – Trolox equivalents).

Genotype	Trolox Antioxidant Capacity (mmol TE/100 g FW) at 15 min	Trolox Antioxidant Capacity (mmol TE/100 g DW) at 15 min
J-21-78	2.19 ± 0.06 f-h (31,9)	13.55 ± 0.36 c-e (34,10)
J-22-14	2.37 ± 0.12 f-l (23,5)	16.42 ± 0.81 g-j (22,4)
J-41-83	2.15 ± 0.12 e-g (32,10)	13.96 ± 0.72 c-e (33,9)
J-42-45	2.31 ± 0.10 f-j (26,6)	15.30 ± 0.50 e-h (26,5)
J-43-87	2.45 ± 0.14 f-l (19,3)	16.61 ± 0.82 f-j (17,3)
J-444-39	2.66 ± 0.11 j-o (12,2)	17.94 ± 0.52 i-l (7,2)
J-45-14	1.79 ± 0.09 d (35,11)	11.93 ± 0.54 bc (38,11)
J-46-55	2.40 ± 0.17 f-k (21,4)	15.01 ± 0.95 d-g (27,6)
J-56-18	2.81 ± 0.08 no (7,1)	18.41 ± 0.26 k-n (5,1)
J-66-53	1.48 ± 0.12 bc (37,12)	9.25 ± 0.92 a (40,12)
J-73-39	2.23 ± 0.13 f-i (29,7)	14.92 ± 0.80 d-g (28,7)
K-3-03	2.53 ± 0.11 j-n (17,5)	17.99 ± 0.59 i-m (6,5)
K-3-05	2.70 ± 0.11 m-o (9,3)	19.59 ± 0.61 mn (3,3)
K-3-06	2.81 ± 0.11 no (8,2)	19.98 ± 0.54 n (1,1)
K-3-07	2.69 ± 0.11 l-o (10,4)	18.53 ± 0.51 k-n (4,4)
K-97-12	2.93 ± 0.21 op (3,1)	19.82 ± 1.20 l-n (2,2)
R-2-06	2.33 ± 0.18 f-n (25,10)	16.78 ± 0.95 f-l (15,7)
R-2-07	2.40 ± 0.11 h-o (22,8)	15.99 ± 0.57 f-k (25,11)
R-2-10	2.46 ± 0.05 j-o (18,7)	16.23 ± 0.39 f-k (23,10)
R-2-11	2.29 ± 0.12 f-m (27,11)	16.51 ± 0.64 f-k (20,9)
R-2-13	2.84 ± 0.56 i-q (5,2)	17.03 ± 1.33 d-n (13,5)
R-2-14	2.35 ± 0.11 f-n (24,9)	17.92 ± 0.28 h-n (8,1)

[1]Genotypes not connected by the same letter are statistically different ($p < 0.05$) based on linear contrasts extracted from linear mixed models. In brackets, overall rank followed by group rank (J-PP ranked with Japanese and U of S cultivars ranked with Russian group).

Appendix D.6. Continued. Foundation Germplasm: Phenotypic average[1] +/- SE and rankings for Trolox antioxidant capacity assay at 15 min assay duration in blue honeysuckle and comparison crops in 2012/2013 in the Fraser Valley, BC, Canada (n=18, J – Japanese, K – Kuril, R – Russian, FW – fresh weight, DW – dry weight, TE – Trolox equivalents).

Genotype	Trolox Antioxidant Capacity (mmol TE/100 g FW) at 15 min	Trolox Antioxidant Capacity (mmol TE/100 g DW) at 15 min.
R-2-16	3.27 ± 0.11 q (1,1)	17.89 ± 0.40 j-n (9,2)
R-27-35	2.68 ± 0.17 l-o (11,3)	16.92 ± 0.79 h-k (14,6)
J-PP	2.22 ± 0.11 f-j (30,8)	14.63 ± 0.67 d-g (31,8)
'Borealis'	2.53 ± 0.22 j-o (16,6)	17.49 ± 0.62 i-l (11,4)
'Tundra'	2.58 ± 0.09 k-o (15,5)	17.73 ± 0.36 i-n (10,3)
'Indigo Gem'	2.62 ± 0.09 l-o (13,4)	16.66 ± 0.34 h-k (16,8)
Blueberry		
'Bluecrop'	2.26 ± 0.23 f-j (28,3)	12.42 ± 0.97 bc (36,3)
'Duke'	2.43 ± 0.15 g-m (20,2)	14.68 ± 0.64 d-g (30,2)
'Elliott'	3.17 ± 0.27 pq (2,1)	16.05 ± 0.97 f-i (24,1)
'Reka'	1.84 ± 0.18 de (34,4)	11.12 ± 0.78 ab (39,4)
Raspberry		
'Cascade Bounty'	2.14 ± 0.13 f (33,4)	16.54 ± 0.46 g-j (19,2)
'Chemainus'	2.81 ± 0.10 no (6,2)	17.48 ± 0.55 i-k (12,1)
'Meeker'	2.86 ± 0.09 op (4,1)	16.50 ± 0.65 g-j (21,3)
'Saanich'	2.61 ± 0.13 k-o (14,3)	14.89 ± 0.61 d-g (29,4)
Strawberry		
'Puget Reliance'	1.22 ± 0.10 ab (39,3)	13.17 ± 1.29 cd (35,3)
'Rainier'	1.16 ± 0.11 a (40,4)	12.33 ± 1.18 bc (37,4)
'Stolo'	1.43 ± 0.06 a-c (38,2)	14.58 ± 0.77 d-f (32,2)
'Totem'	1.64 ± 0.05 cd (36,1)	16.57 ± 0.54 g-j (18,1)

[1]Genotypes not connected by the same letter are statistically different ($p < 0.05$) based on linear contrasts extracted from linear mixed models. In brackets, overall rank followed by group rank (J-PP ranked with Japanese and U of S cultivars ranked with Russian group).

Appendix D.7. Foundation Germplasm: Phenotypic average[1] +/- SE and rankings for ferric reducing antioxidant potential assay at 14 min assay duration in blue honeysuckle and comparison crops in 2012/2013 in the Fraser Valley, BC, Canada (n=18, J – Japanese, K – Kuril, R – Russian, FW – fresh weight, DW – dry weight, AAE – ascorbic acid equivalents).

Genotype	Ferric Reducing Antioxidant Potential (mmol AAE/100 g FW) at 14 min	Ferric Reducing Antioxidant Potential (mmol AAE/100 g DW) at 14 min
J-21-78	6.38 ± 0.19 c-f (27,8)	39.43 ± 0.87 e-h (29,10)
J-22-14	6.62 ± 0.22 d-i (23,5)	45.82 ± 1.49 l-n (19,4)
J-41-83	5.89 ± 0.17 b-e (32,11)	38.30 ± 0.94 c-g (31,11)
J-42-45	6.66 ± 0.39 e-i (22,4)	44.01 ± 1.78 j-l (22,5)
J-43-87	7.18 ± 0.23 g-j (15,3)	48.66 ± 0.92 m-p (16,3)
J-444-39	7.31 ± 0.44 h-k (13,2)	49.10 ± 2.19 n-p (15,2)
J-45-14	5.94 ± 0.12 b-d (31,10)	39.82 ± 0.51 e-h (28,9)
J-46-55	6.40 ± 0.18 c-f (25,6)	40.37 ± 1.15 f-i (27,8)
J-56-18	8.51 ± 0.31 m-o (6,1)	55.65 ± 1.38 rs (7,1)
J-66-53	5.89 ± 0.27 b-e (33,12)	36.14 ± 1.40 b-e (33,12)
J-73-39	6.38 ± 0.26 c-f (26,7)	42.78 ± 1.14 h-l (24,6)
K-3-03	7.53 ± 0.24 j-l (12,2)	53.62 ± 1.08 qr (9,2)
K-3-05	7.02 ± 0.25 f-j (17,4)	51.02 ± 1.22 pq (10,3)
K-3-06	6.91 ± 0.26 f-j (18,5)	49.20 ± 1.20 n-p (14,5)
K-3-07	7.17 ± 0.33 h-j (16,3)	49.30 ± 1.26 op (13,4)
K-97-12	8.61 ± 0.74 m-o (5,1)	58.38 ± 4.82 s (5,1)
R-2-06	7.63 ± 0.33 i-m (11,8)	55.04 ± 1.41 q-s (8,6)
R-2-07	6.85 ± 0.17 f-j (20,10)	45.80 ± 0.95 k-o (20,10)
R-2-10	7.65 ± 0.15 j-m (10,7)	50.47 ± 1.11 o-q (11,7)
R-2-11	6.69 ± 0.32 d-j (21,11)	48.45 ± 2.10 m-p (17,9)
R-2-13	9.86 ± 1.31 o-q (2,2)	59.62 ± 0.70 r-t (2,2)
R-2-14	7.70 ± 0.43 h-m (9,6)	58.84 ± 2.89 rs (3,3)

[1]Genotypes not connected by the same letter are statistically different ($p < 0.05$) based on linear contrasts extracted from linear mixed models. In brackets, overall rank followed by group rank (J-PP ranked with Japanese and U of S cultivars ranked with Russian group).

Appendix D.7. Continued. Foundation Germplasm: Phenotypic average[1] +/- SE and rankings for ferric reducing antioxidant potential assay at 14 min assay duration in blue honeysuckle and comparison crops in 2012/2013 in the Fraser Valley, BC, Canada (n=18, J – Japanese, K – Kuril, R – Russian, FW – fresh weight, DW – dry weight, AAE – ascorbic acid equivalents).

Genotype	Ferric Reducing Antioxidant Potential (mmol AAE/100 g FW) at 14 min	Ferric Reducing Antioxidant Potential (mmol AAE/100 g DW) at 14 min
R-2-16	10.52 ± 0.39 q (1,1)	57.46 ± 1.27 rs (6,5)
R-27-35	6.88 ± 0.17 f-j (19,9)	43.84 ± 0.92 i-l (23,11)
J-PP	6.35 ± 0.20 c-g (29,9)	41.86 ± 1.06 g-k (25,7)
'Borealis'	8.32 ± 0.35 l-n (7,4)	58.80 ± 1.34 s (4,4)
'Tundra'	9.74 ± 0.39 pq (3,3)	66.90 ± 1.66 t (1,1)
'Indigo Gem'	7.95 ± 0.45 k-m (8,5)	50.16 ± 1.33 o-q (12,8)
Blueberry		
'Bluecrop'	6.06 ± 0.23 b-e (30,3)	33.86 ± 0.74 ab (38,4)
'Duke'	6.37 ± 0.31 c-g (28,2)	38.59 ± 0.84 d-g (30,2)
'Elliott'	9.12 ± 0.63 n-p (4,1)	46.09 ± 1.32 l-o (18,1)
'Reka'	5.52 ± 0.20 b (35,4)	34.08 ± 0.65 ab (36,3)
Raspberry		
'Cascade Bounty'	5.51 ± 0.45 b (36,4)	41.69 ± 1.97 g-j (26,2)
'Chemainus'	7.25 ± 0.20 ij (14,1)	45.10 ± 1.07 k-m (21,1)
'Meeker'	6.50 ± 0.26 d-h (24,2)	37.64 ± 1.98 c-f (32,3)
'Saanich'	5.81 ± 0.19 bc (34,3)	33.16 ± 0.85 ab (39,4)
Strawberry		
'Puget Reliance'	3.25 ± 0.11 a (39,3)	34.01 ± 1.18 ab (37,3)
'Rainier'	3.38 ± 0.09 a (38,2)	35.75 ± 1.08 b-d (34,1)
'Stolo'	3.18 ± 0.09 a (40,4)	32.15 ± 0.62 a (40,4)
'Totem'	3.49 ± 0.14 a (37,1)	34.96 ± 0.82 a-c (35,2)

[1]Genotypes not connected by the same letter are statistically different (p < 0.05) based on linear contrasts extracted from linear mixed models. In brackets, overall rank followed by group rank (J-PP ranked with Japanese and U of S cultivars ranked with Russian group).

Appendix D.8. Foundation Germplasm: Comparisons based on linear contrasts extracted from linear mixed model regression of parent genotypes used in hybrid cross combinations to make improved families for biochemical determinations of fruit quality in blue honeysuckle in 2012/2013 in Chilliwack, BC, Canada ($p < 0.05$, n=6).

		Kuril vs. Japanese	Japanese vs. Russian	Russian vs. Kuril
Dry Matter (%)	Lower	6	1	0
	Equal	2	9	5
	Greater	0	6	11
Total Soluble Solids (%)	Lower	2	1	0
	Equal	6	10	13
	Greater	0	5	3
Titratable Acidity (% Citric Acid Equivalents)	Lower	5	12	6
	Equal	2	1	6
	Greater	1	3	4
pH	Lower	1	1	7
	Equal	5	8	4
	Greater	2	7	5
Total Soluble Solids:Titratable Acidity	Lower	2	0	2
	Equal	1	3	6
	Greater	5	13	8

Appendix D.8. Continued. Foundation Germplasm: Comparisons based on linear contrasts extracted from linear mixed model regression of parent genotypes used in hybrid cross combinations to make improved families for biochemical determinations of fruit quality in blue honeysuckle in 2012/2013 in Chilliwack, BC, Canada ($p < 0.05$, n=6).

		Kuril vs. Japanese	Japanese vs. Russian	Russian vs. Kuril
Total Phenolics (mg Gallic Acid Equivalents/100 g fresh weight)	Lower	0	2	0
	Equal	8	12	16
	Greater	0	2	0
Total Phenolics (mg Gallic Acid Equivalents/100 g dry weight)	Lower	0	0	0
	Equal	7	16	16
	Greater	1	0	0
Trolox Antioxidant Capacity (mmol Trolox Equivalents/100 g fresh weight) at 5 min	Lower	0	0	0
	Equal	1	6	15
	Greater	7	10	1
Trolox Antioxidant Capacity (mmol Trolox Equivalents/100 g dry weight) at 5 min	Lower	0	0	0
	Equal	2	10	16
	Greater	6	6	0
Ferric Reducing Antioxidant Potential (mmol Ascorbic Acid Equivalents/100 g fresh weight) at 4 min	Lower	0	0	0
	Equal	0	1	4
	Greater	8	15	12
Ferric Reducing Antioxidant Potential (mmol Ascorbic Acid Equivalents/100 g dry weight) at 4 min	Lower	0	0	0
	Equal	1	2	12
	Greater	7	14	4

Appendix D.9. Improved Germplasm: Statistical classification of blue honeysuckle hybrids compared with their parent foundation genotypes for biochemical determinations of fruit quality in blue honeysuckle in 2012/2013 in Chilliwack, BC, Canada (n=6[1]).

		Low			High		Total
		Transgressive Segregants	Parent Types	Intermediates	Parent Types	Transgressive Segregants	Transgressive Segregants
Dry Matter (%)	All Improved	4.4	31.3	30.6	26.3	7.5	11.9
	Japanese/Kuril	3.1	25.0	15.6	34.4	21.9	25.0
	Japanese/Russian	7.8	42.2	34.4	10.9	4.7	12.5
	Kuril/Russian	1.6	23.4	34.4	37.5	3.1	4.7
Total Soluble Solids (%)	All Improved	1.9	13.1	60.0	23.1	1.9	3.8
	Japanese/Kuril	3.1	12.5	59.4	21.9	3.1	6.3
	Japanese/Russian	3.1	14.1	57.8	23.4	1.6	4.7
	Kuril/Russian	0.0	12.5	62.5	23.4	1.6	1.6
Titratable Acidity (% Citric Acid Equivalents)	All Improved	8.8	20.6	25.6	28.8	16.3	25.0
	Japanese/Kuril	0.0	25.0	9.4	40.6	25.0	25.0
	Japanese/Russian	20.3	20.3	26.6	21.9	10.9	31.3
	Kuril/Russian	1.6	18.8	32.8	29.7	17.2	18.8
pH	All Improved	5.0	25.6	31.9	25.6	11.9	16.9
	Japanese/Kuril	9.4	28.1	40.6	15.6	6.3	15.6
	Japanese/Russian	4.7	31.3	28.1	21.9	14.1	18.8
	Kuril/Russian	3.1	18.8	31.3	34.4	12.5	15.6
Total Soluble Solids:Titratable Acidity	All Improved	15.0	28.8	29.4	16.9	10.0	25.0
	Japanese/Kuril	31.3	25.0	25.0	12.5	6.3	37.5
	Japanese/Russian	9.4	26.6	28.1	20.3	15.6	25.0
	Kuril/Russian	12.5	32.8	32.8	15.6	6.3	18.8

[1]Comparisons made by pairwise comparison using linear contrasts extracted from mixed regression models (p<0.05).

Appendix D.10. Foundation and Improved Germplasm: Phenotypic averages for additional antioxidant activity assay durations in blue honeysuckle and comparison crops in 2012/2013 in the Fraser Valley, BC, Canada (FW – fresh weight, DW – dry weight, TE – Trolox equivalents, AAE – ascorbic acid equivalents).

	Group	Japanese	Kuril	Russian	Japanese/ Kuril	Japanese/ Russian	Kuril/ Russian	Blue- berry	Rasp- berry	Straw- berry
	Trolox Antioxidant Capacity									
mmol TE/100 g FW at 15 min	Average	1.86	2.21	2.14	2.12	2.33	2.66	1.62	2.50	1.34
	Median	1.76	2.21	2.22	2.14	2.31	2.71	1.60	2.55	1.34
	Minimum	1.51	2.06	1.72	0.81	1.19	1.74	1.00	2.25	1.13
	Maximum	2.31	2.34	2.41	2.93	3.15	3.50	2.29	2.64	1.54
	Range	0.79	0.28	0.69	2.12	1.97	1.76	1.29	0.39	0.41
mmol TE/100 g DW at 15 min	Average	12.46	16.22	13.78	15.13	16.52	19.35	10.51	16.39	13.06
	Median	11.88	16.33	14.03	14.67	16.97	18.98	10.52	16.80	13.17
	Minimum	9.59	15.43	12.48	5.67	7.91	11.62	7.20	14.38	11.46
	Maximum	15.81	16.62	14.73	24.48	27.89	30.62	13.81	17.59	14.43
	Range	6.22	1.19	2.25	18.80	19.98	19.01	6.61	3.20	2.97
	Ferric Reducing Antioxidant Potential									
mmol AAE/100 g FW at 14 min	Average	5.80	6.90	7.94	6.05	6.97	7.68	5.28	6.19	3.24
	Median	5.72	6.87	7.97	6.05	6.88	7.72	5.06	6.45	3.33
	Minimum	5.02	5.98	7.05	3.62	4.33	5.31	3.98	5.35	2.80
	Maximum	6.74	7.85	9.46	7.76	12.69	11.00	7.02	6.50	3.50
	Range	1.72	1.87	2.41	4.14	8.36	5.69	3.03	1.15	0.70
mmol AAE/100 g DW at 14 min	Average	38.73	50.49	51.13	43.27	49.51	55.83	34.40	40.81	31.41
	Median	39.24	50.82	51.77	42.21	48.48	55.00	33.16	41.60	32.16
	Minimum	31.32	44.72	43.27	25.56	28.96	35.42	29.02	34.16	28.94
	Maximum	45.84	54.14	56.83	65.01	92.61	88.14	42.26	45.90	32.39
	Range	14.52	9.42	13.55	39.46	63.66	52.72	13.24	11.74	3.46

Appendix D.11. Improved Germplasm: Statistical classification[1] (%) of hybrids compared with their parent foundation genotypes for biochemical determinations of nutritional content in blue honeysuckle in 2012/2013 in Chilliwack, BC, Canada (n=6, FW – fresh weight, DW – dry weight, GAE – gallic acid equivalents, TE – Trolox equivalents, AAE -ascorbic acid equivalents).

		Low			High		Total
		Transgressive Segregants	Parent Types	Intermediates	Parent Types	Transgressive Segregants	Transgressive Segregants
Total Phenolics (mg GAE/100 g FW)	All Improved	5.6	8.8	48.8	15.6	21.3	26.9
	Japanese/Kuril	21.9	18.8	40.6	3.1	15.6	37.5
	Japanese/Russian	3.1	10.9	57.8	20.3	7.8	10.9
	Kuril/Russian	0.0	1.6	43.8	17.2	37.5	37.5
Total Phenolics (mg GAE/100 g DW)	All Improved	9.4	5.6	48.8	10.6	25.6	35.0
	Japanese/Kuril	40.6	18.8	15.6	6.3	18.8	59.4
	Japanese/Russian	3.1	4.7	64.1	12.5	15.6	18.8
	Kuril/Russian	0.0	0.0	50.0	10.9	39.1	39.1

[1]Comparisons made by pairwise comparison using linear contrasts extracted from mixed regression models (p<0.05).

Appendix D.11. Continued. Improved Germplasm: Statistical classification[1] (%) of hybrids compared with their parent foundation genotypes for biochemical determinations of nutritional content in blue honeysuckle in 2012/2013 in Chilliwack, BC, Canada (n=6, FW – fresh weight, DW – dry weight, GAE – gallic acid equivalents, TE – Trolox equivalents, AAE -ascorbic acid equivalents).

		Low			High		Total
		Transgressive Segregants	Parent Types	Intermediates	Parent Types	Transgressive Segregants	Transgressive Segregants
Trolox Antioxidant Capacity (mmol TE/100 g FW) at 5 minutes	All Improved	11.3	19.4	45.6	19.4	4.4	15.6
	Japanese/Kuril	12.5	31.3	25.0	31.3	0.0	12.5
	Japanese/Russian	14.1	20.3	34.4	29.7	1.6	15.6
	Kuril/Russian	7.8	12.5	67.2	3.1	9.4	17.2
Trolox Antioxidant Capacity (mmol TE/100 g DW) at 5 minutes	All Improved	11.3	11.9	50.6	22.5	3.8	15.0
	Japanese/Kuril	15.6	21.9	40.6	21.9	0.0	15.6
	Japanese/Russian	15.6	12.5	31.3	37.5	3.1	18.8
	Kuril/Russian	4.7	6.3	75.0	7.8	6.3	10.9
Ferric Reducing Antioxidant Potential (mmol AAE/100 g FW) at 4 minutes	All Improved	10.6	42.5	26.9	16.9	3.1	13.8
	Japanese/Kuril	12.5	34.4	25.0	25.0	3.1	15.6
	Japanese/Russian	12.5	48.4	31.3	7.8	0.0	12.5
	Kuril/Russian	7.8	40.6	23.4	21.9	6.3	14.1
Ferric Reducing Antioxidant Potential (mmol AAE/100 g DW) at 4 minutes	All Improved	13.1	21.9	41.3	18.8	5.0	18.1
	Japanese/Kuril	9.4	31.3	40.6	18.8	0.0	9.4
	Japanese/Russian	15.6	25.0	35.9	23.4	0.0	15.6
	Kuril/Russian	12.5	14.1	46.9	14.1	12.5	25.0

[1]Comparisons made by pairwise comparison using linear contrasts extracted from mixed regression models (p<0.05).