

# Spring phenological adaptation of improved blue honeysuckle (*Lonicera caerulea* L.) germplasm to a temperate climate

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**Abstract** The blue honeysuckle (*Lonicera caerulea* L.) has outstanding features as a novel fruit crop, including extreme winter hardiness, resistance of flowers to severe frosts and early season phenology. Its northern climatic adaptation also limits its range of production. Therefore, crop enhancement requires development of germplasm with adaptation to temperate climatic regions suited to large-scale horticulture. In a cold continental climate, the University of Saskatchewan fruit breeding program utilizes a wide-cross breeding strategy to produce improved germplasm groups from foundation groups from Russia, Japan and the Kuril Islands. A key objective is to evaluate temperate climate adaptation in these improved groups compared to their parental foundation genotypes. In a temperate climate in the Fraser Valley, British Columbia, Canada, evaluation of spring phenology in 2012 and 2013 compared blue

honeysuckle to blueberry, raspberry and strawberry. By determining the range of variation within improved groups and the general mode of gene action controlling phenological traits, the current study characterized methods to enhance temperate climate adaptation through breeding. The improved groups generated from wide crosses exhibited hybrid vigour for numerous traits, presenting opportunities for broadening the crop's range of production. Selection for enhanced adaptation will be possible due to prevalence of intermediate types between the phenological extremes seen in the Russian and Kuril groups, moderation of these extremes by the Japanese group's intermediate phenology through dominant and overdominant gene action and high broad-sense heritability. Long-term genetic gains are most feasible for combinations of Japanese and Kuril groups, especially in bloom phenology.

**Keywords** Bloom · Bud break · Genetic resources · Harvest · Haskap · Honeyberry

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## Introduction

Blue honeysuckle is a novel fruit crop comprised of the polymorphic, tetraploid ssp. of *Lonicera caerulea* L., including ssp. *kamtschatica*, *edulis*, *emphylocalyx* and *villosa* (Plekhanova and Rostova 1994). Alternate common names include honeyberry

in the USA and haskap in Japan and Canada, but blue honeysuckle is more inclusive of global crop genetic resources. With a circumpolar geographic distribution, blue honeysuckle is found mostly in the boreal and arctic forest belts of Eurasia where it grows as a woody perennial bush, 0.5–4.0 m in height (Rudenberg and Green 1969). 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, 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, except BC, and northern parts of the United States (Bors et al. 2012; Fernald and Kinsey 1943).

The primary distribution of blue honeysuckle is in boreal and temperate coniferous woodlands, shrublands, fens and marshes as forest undergrowth (Mucina 1997). As is typical for northern circumpolar Lonicerans (Rudenberg and Green 1969), 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 sub-alpine and alpine belts at its southern extremes (Rudenberg and Green 1969). 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).

The provenance of important foundation germplasm groups are primarily very cold climates of Russia, Japan and the Kuril Islands, but wild relatives are also found in the boreal belt of North America (Peel et al. 2007; Pojarkova 1958). Breeding programs began to enhance blue honeysuckle in Russia in the 1950's (Sabitov 1986) and in Japan in the 1967 (Nakajima 1996). More recently, an increase in global interest in the crop began with importation of germplasm to North America. In North America, breeding is underway in Oregon, USA (Thompson 2006) and Saskatchewan, Canada (Bors et al. 2012), the latter at the University of Saskatchewan (U of S) in Saskatoon.

Some of the crop's important features are its extremely early phenology and cold hardiness and the fruit's high antioxidant content, unique flavours and aromas and diversity of shapes (Thompson and Barney 2007). With general adaptation to cold, continental climates, the blue honeysuckle's suitability for temperate climates is questionable due to low chilling requirement and early bud break during fluctuating winter temperatures (Plekhanova 1986). Breeding of blue honeysuckle cvs. with adaptation to temperate climates is important for expanding its range of production and facilitating its development as a commercial horticultural crop (Thompson 2006).

In addition to understanding genetic diversity for important traits related to phenological adaptation in three important foundation germplasm groups (unpublished data), a key research objective is to determine the ability to make genetic progress in three improved germplasm groups. Therefore, to develop judicious 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.

## Materials and methods

Groups of four full-siblings (i.e., families) were selected from each of 40 seedling populations (160 improved hybrid genotypes) produced from combinations of 24 foundation germplasm genotypes. Three unique combinations of foundation groups were each represented by both directions of cross and treated as combined improved groups (i.e.,

Japanese  $\times$  Kuril + Kuril  $\times$  Japanese – Japanese/Kuril, Japanese  $\times$  Russian + Russian  $\times$  Japanese – Japanese/Russian, Kuril  $\times$  Russian + Russian  $\times$  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 1). 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 foundation genotypes as parents of improved genotypes (Table 2). Blue honeysuckle seedling populations at the horticulture field facility at the U of S in Saskatoon, Saskatchewan were used to collect softwood cuttings during active growth on May 20, 2010. Clones were rooted in a heated mist-bed before being transferred to individual plug trays in Sunshine Mix #4 (Sun Gro Horticulture, Agawam, MA, USA).

To compare improved germplasm with parental foundation groups, a site in Chilliwack (49°08'N 121°56'W; 15 m above sea level) was used to establish a field trial. This site's ten-year average annual precipitation was 1.679 m while 2.3 and 18.4 °C were average temperatures in the coldest and warmest months, respectively (The Weather Network 2015). Each of three randomized blocks 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. A first set of plants from Saskatchewan were grown in 11.4 cm deep (142 mL) plug trays (T.O. Plastics, Clearwater, MN, USA). When plants had 25 cm of top growth they were transported to the Fraser Valley on August 28, 2010. These were used to establish the first sub-replicate clone of each genotype per replication. Cuttings that took longer to root were potted in 2.6 L #1 round pots (ITML Horticultural Products,

**Table 1** Blue honeysuckle improved germplasm and comparison crop cultivars compared in the Fraser Valley, BC, Canada

A				B				
Parental cross combination	Seedling families	Siblings/family	Total		Cultivar	Harvest period	Fresh market	Process market
Japanese $\times$ Kuril	5	4	20	Blueberry	'Bluecrop'	Mid	✓	✓
Kuril $\times$ Japanese	3	4	12		'Duke'	Early	✓	✓
Total Japanese/Kuril	8		32		'Elliott'	Late	✓	
				Raspberry	'Reka'	Early		✓
Russian $\times$ Japanese	8	4	32		'Cascade Bounty'	Late		✓
Japanese $\times$ Russian	8	4	32		'Chemainus'	Mid	✓	✓
Total Japanese/Russian	16		64		'Meeker'	Mid		✓
				Strawberry	'Saanich'	Mid	✓	✓
Kuril $\times$ Russian	8	4	32		'Rainier'	Late	✓	✓
Russian $\times$ Kuril	8	4	32		'Puget Reliance'	Early	✓	✓
Total Kuril/Russian	16		64		'Stolo'	Mid	✓	
Grand total	40		160		'Totem'	Mid	✓	✓

(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

**Table 2** Male and female foundation blue honeysuckle genotypes used to produce 40 improved hybrid families selected from the University of Saskatchewan breeding program for evaluation in the Fraser Valley, BC, Canada

	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	Kuril/Russian	KR-KR7	SX-3-06	SX-2-11
	JK-GH4	MT-56-18	SX-3-07		KR-KR5	SX-3-06	SX-2-13
Japanese/Russian	JR-100	MT-21-78	MT-27-35	KR-2	SX-3-06	SX-2-13	
	JR-GH11	MT-444-39	SX-2-16	KR-KR11	SX-3-06	SX-2-06	
	JR-GH5	MT-56-18	SX-2-16	KR-7-10	SX-3-03	SX-2-10	
	JR-GH18	MT-41-83	SX-2-06	KR-7-12	SX-3-03	SX-2-13	
	JR-GH14	MT-66-53	SX-2-16	KR-7-14	SX-3-03	SX-2-16	
	JR-GH25	MT-73-39	SX-2-16	KR-7-13	SX-3-03	SX-2-14	
	JR-GH22	MT-22-14	SX-2-06	RK-T12	SX-2-16	SX-3-06	
	JR-GH23	MT-43-87	SX-2-06	RK-V6	SX-2-06	SX-3-05	
	RJ-J2	SX-2-07	MT-66-53	RK-R6	SX-2-06	SX-3-06	
	RJ-B7	SX-2-13	MT-66-53	RK-V12	SX-2-11	SX-97-12	
	RJ-B2	SX-2-10	MT-73-39	RK-T18	SX-2-11	SX-3-05	
	RJ-J7	SX-2-13	MT-41-83	RK-V18	SX-2-16	SX-3-07	
	RJ-T9	SX-2-16	MT-73-39	RK-T6	SX-2-14	SX-97-12	
	RJ-V4	SX-2-06	MT-444-39	RK-R12	SX-2-07	SX-3-07	
	RJ-B9	SX-2-13	MT-56-18				
	RJ-J4	SX-2-07	MT-444-39				

Branford, ON, Canada) and grown in a greenhouse from September 1, 2010 to January 21, 2011. When these plants had approximately 45 cm of top growth, dormancy was artificially induced through application of short-day (8 h) photoperiod at 0–2 °C temperature. In this state, plants were transported to the Fraser Valley and planted from April 16–18, 2011. These plants were used to complete each sub-plot. Spacing was 0.6 m within-rows and between-row spacing was 1.8 with 0.5 m hilled beds. Row orientation was east/west and inter-row space managed via perennial grass ground cover. Bird netting was used to protect fruit development and harvest.

Standard cvs. of northern highbush blueberry (*Vaccinium corymbosum* L.), floricane-fruiting red raspberry (*Rubus idaeus* L.) and June-bearing strawberry (*Fragaria x ananassa* Duchesne.) were included to compare to blue honeysuckle germplasm (Table 1). Raspberry and strawberry plants were procured as dormant bare-root plants from Norcal Nursery Inc. (Burlington, WA, USA), whereas blueberry plants had 45 cm of top

growth and were grown in 2.6 L pots obtained from JRT Nurseries Inc. (Aldergrove, BC, Canada).

From January, 2012 to December, 2013, spring phenology was observed at two to four day intervals for each plant independently. Julian dates were recorded for three determinations of bud break (bud scales peeled back, releasing green tissues for 10, 50 and 90% of buds), flowering onset (corolla open for first pair of flowers, 30 and 90% of first flowers on new shoots) and fruit colouring (50, 75 and 100% of fully blue fruit) as well as the date of a single, simultaneous harvest from each plant (3–5 days following 10% blue fruit, depending on weather conditions). Multiple harvests were required for blueberry, raspberry and strawberry fruit, and both the initial and final harvest dates were determined (Fig. 1).

General interpretations of trends between and within blue honeysuckle groups and comparison crops were made using summary statistics, and density plots were used to compare the distributions of observations for each improved group. Analysis using linear mixed



**Fig. 1** 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. **i** 50% blue fruit, **j** 75% blue fruit, **k** 100% blue fruit, which was followed by synchronous harvest of all fruit per plant 3–5 days later. **l** Active shoot growth during early fruit development

model regression in the ‘R’ statistical environment (R Development Core Team 2015) was conducted using the ‘lme4’ package (Bates et al. 2015). Block averages for each genotype were calculated from three independently-observed sub-replicate clones and then block and year were treated as random factors. Mixed models were used to produce linear contrasts that were subjected to pairwise comparisons to determine statistically significant differences ( $p < 0.05$ ) between genotypes using the ‘multcompView’ package (Graves et al. 2015). The parent foundation 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 siblings were compared to their parents for placement in one of five statistical categories:

- Early transgressive segregant if significantly earlier than both parents;
- Early-parent type if significantly earlier than one parent but equivalent to the other;
- Intermediate type if not different from either parent or statistically earlier than one and statistically later than the other;
- Late-parent type if significantly later than one parent but equivalent to the other;
- Late transgressive segregant if significantly later 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. For narrow-sense heritability ( $h^2$ ), the mid-parent value for each hybrid genotype was calculated and mid-parent regression applied using genotypic averages. The degree of heritability and the strength of correlations were interpreted heuristically.

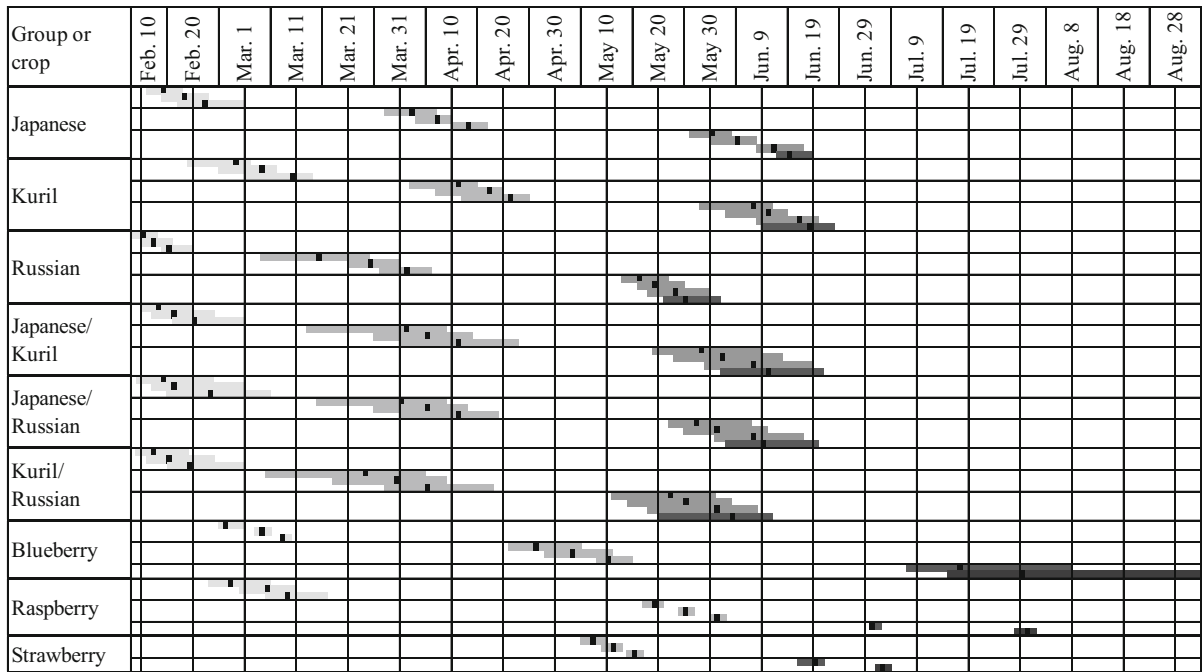
## Results and discussion

### 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 (Fig. 2; Table 3). Even the latest genotype was far earlier than is reported for Russian germplasm in Russian environments, which range from March 15 in the Kaluga oblast (Esichev 2009) to April and May in the Tomaskaya oblast (Suchkova and Senina 2009). 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). As for bud break, flowering onset was much earlier in the Fraser Valley than for Russian germplasm observed in Russian climates such as the Komi Republic (Ryabina 2009) and the Primorye oblast (Stepanova 2009). 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 5). In contrast with bud break and flowering onset, fruit colouring in the Fraser Valley showed some overlap with reports of Russian germplasm in Russian regions such as the Mari El Republic (Golovunin 2009) and Pavlovsk (Plekhanova 2000). 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 6). 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



**Fig. 2** Spring phenology in blue honeysuckle foundation and improved groups 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

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 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. 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

**Table 3** Bud break phenophase in blue honeysuckle groups and comparison crops in 2012/2013 in Chilliwack, BC, Canada (n = 6)

Group #	Japanese 11	Kuril 5	Russian 8	Japanese/Kuril 32	Japanese/Russian 64	Kuril/Russian 64	Blueberry 4	Raspberry 4
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

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.

#### 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 (Tables 3, 4, 5). 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 (Fig. 3; Table 7). 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



**Table 4** Flowering onset phenophase in blue honeysuckle groups and comparison crops in 2012/2013 in Chilliwack, BC, Canada (n = 6)

Group #	Japanese	Kuril	Russian	Japanese/ Kuril	Japanese/ Russian	Kuril/ Russian	Blue- berry	Rasp- berry	Straw- berry
	11	5	8	32	64	64	4	4	4
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	3.3
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	3.2
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	2.2

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 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

**Table 5** Fruit colouring/harvest phenophases in blue honeysuckle groups foundation and improved groups and comparison crops in 2012/2013 in Chilliwack, BC, Canada (n = 6)

Group #S	Japanese 11	Kuril 5	Russian 8	Japanese/Kuril 32	Japanese/Russian 64	Kuril/Russian 64
50% blue fruit						
Average	May. 30	Jun. 7	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
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
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
Sole harvest for blue honeysuckle						
Average	Jun. 14	Jun. 18	May. 25	Jun. 10	Jun. 9	Jun. 3
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 #	Blueberry 4		Raspberry 4		Strawberry 4	
First harvest for comparison crops						
Average	Jul. 17		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	
Minimum	Jul. 15		Jul. 28		Jul. 1	
Maximum	Sept. 1		Jul. 31		Jul. 3	
Range (days)	48.1		2.8		2.0	

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.

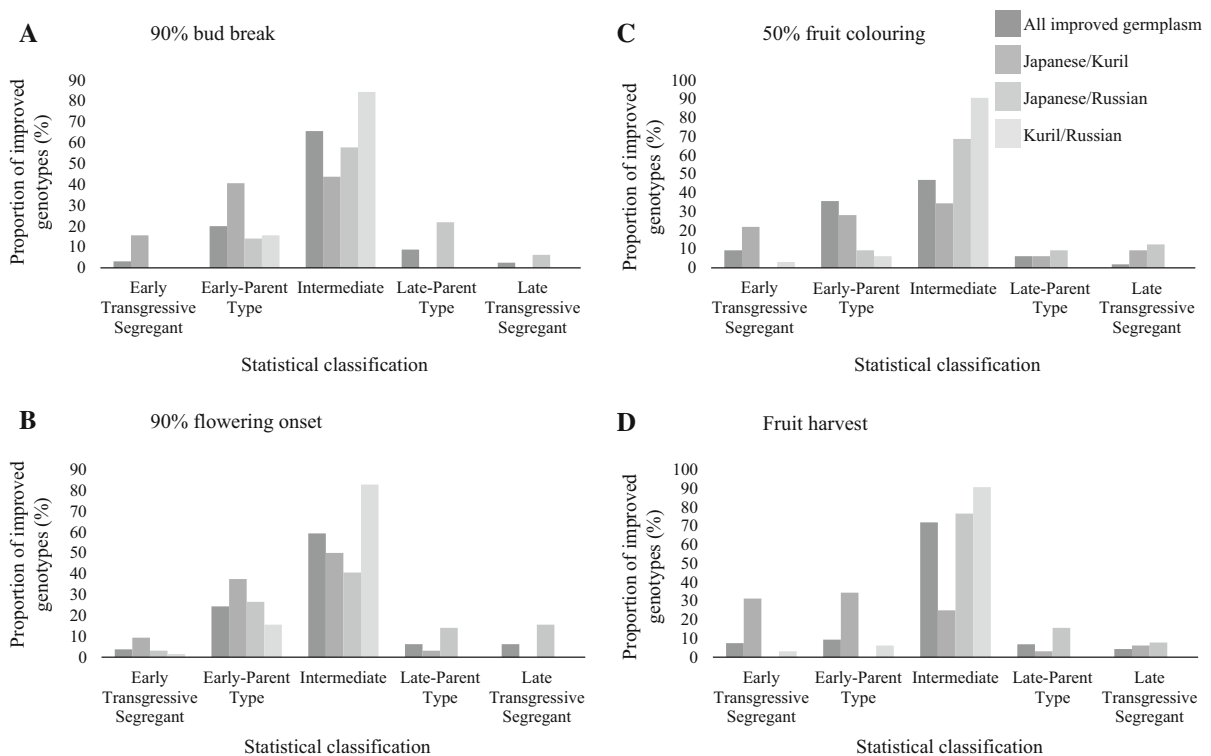
#### Improved Japanese/Russian germplasm

The Japanese/Russian group reached each successive estimate of bud break over a range of 14–17 days

**Table 6** Heritability estimates for spring phenophases across blue honeysuckle groups alone and in combination in 2012/2013 in Chilliwack, BC, Canada

	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	-0.15	0.90	-0.03	0.89	-0.09	0.38	0.56	0.23	0.62	0.82	0.47	0.71	-0.02	0.65	0.00	0.68	-0.10	0.64	-0.11
Japanese/Russian	0.89	0.14	0.89	0.16	0.86	0.19	0.88	-0.09	0.74	0.01	0.90	-0.03	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	-0.02	0.64	-0.03	0.88	-0.07	0.91	-0.05

$H^2$  broad-sense heritability calculated from linear mixed model regression,  $h^2$  narrow-sense heritability (negative heritability estimates (italics) may not represent biologically meaningful values) calculated from mid-parent regression of genotypic averages (different regression models were used to calculate  $H^2$  and  $h^2$  heritability estimates, so these measures are not directly comparable)



**Fig. 3** 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

(Table 3), flowering onset over 17–24 days (Table 4) and fruit colouring/harvest over 15–16 days (Table 5). At bud break, there were some late and no early transgressive segregants, more late- than early-parent types and mostly intermediates (Fig. 3; Table 7). 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 over-dominance 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.

**Table 7** Statistical classification (%) of improved blue honeysuckle hybrids compared with their parental foundation genotypes for spring phenophases in 2012/2013 in Chilliwack, BC, Canada (n = 6)

	Early			Intermediates			Late			Early			Intermediates			Late				
	Transgressive segregants	Parent types	Parent types	Transgressive segregants	Parent types	Parent types	Transgressive segregants	Parent types	Parent types	Transgressive segregants	Parent types	Parent types	Transgressive segregants	Parent types	Parent types	Transgressive segregants	Parent types	Parent types		
All improved	1.9	29.4	55.6	10.6	2.5	18.8	65.6	13.1	0.0	2.5	18.8	65.6	13.1	0.0	2.5	18.8	65.6	13.1	0.0	
10% bud break																				
Japanese/Kuril	9.4	62.5	21.9	6.3	0.0	34.4	56.3	0.0	0.0	9.4	34.4	56.3	0.0	0.0	9.4	34.4	56.3	0.0	0.0	
Japanese/Russian	0.0	17.2	53.1	23.4	6.3	18.8	50.0	31.3	0.0	0.0	18.8	50.0	31.3	0.0	0.0	18.8	50.0	31.3	0.0	
Kuril/Russian	0.0	25.0	75.0	0.0	0.0	10.9	85.9	1.6	0.0	1.6	10.9	85.9	1.6	0.0	1.6	10.9	85.9	1.6	0.0	
All improved	2.5	20.6	67.5	6.9	2.5	16.9	66.9	6.9	5.6	3.8	16.9	66.9	6.9	5.6	3.8	16.9	66.9	6.9	5.6	
50% bud break																				
Japanese/Kuril	12.5	53.1	31.3	3.1	0.0	25.0	56.3	0.0	0.0	18.8	25.0	56.3	0.0	0.0	18.8	25.0	56.3	0.0	0.0	
Japanese/Russian	0.0	10.9	67.2	15.6	6.3	15.6	53.1	17.2	14.1	0.0	15.6	53.1	17.2	14.1	0.0	15.6	53.1	17.2	14.1	
Kuril/Russian	0.0	14.1	85.9	0.0	0.0	14.1	85.9	0.0	0.0	0.0	14.1	85.9	0.0	0.0	0.0	14.1	85.9	0.0	0.0	
All improved	3.1	20.0	65.6	8.8	2.5	24.4	59.4	6.3	6.3	3.8	24.4	59.4	6.3	6.3	3.8	24.4	59.4	6.3	6.3	
90% bud break																				
Japanese/Kuril	15.6	40.6	43.8	0.0	0.0	37.5	50.0	3.1	0.0	9.4	37.5	50.0	3.1	0.0	9.4	37.5	50.0	3.1	0.0	
Japanese/Russian	0.0	14.1	57.8	21.9	6.3	26.6	40.6	14.1	15.6	3.1	26.6	40.6	14.1	15.6	3.1	26.6	40.6	14.1	15.6	
Kuril/Russian	0.0	15.6	84.4	0.0	0.0	15.6	82.8	0.0	0.0	1.6	15.6	82.8	0.0	0.0	1.6	15.6	82.8	0.0	0.0	
All improved	9.4	35.6	46.9	6.3	1.9	8.8	71.9	7.5	4.4	7.5	8.8	71.9	7.5	4.4	7.5	8.8	71.9	7.5	4.4	
50% blue fruit																				
Japanese/Kuril	21.9	28.1	34.4	6.3	9.4	28.1	25.0	6.3	6.3	34.4	28.1	25.0	6.3	6.3	34.4	28.1	25.0	6.3	6.3	
Japanese/Russian	0.0	9.4	68.8	9.4	12.5	0.0	76.6	15.6	7.8	0.0	0.0	76.6	15.6	7.8	0.0	0.0	76.6	15.6	7.8	
Kuril/Russian	3.1	6.3	90.6	0.0	0.0	7.8	90.6	0.0	0.0	1.6	7.8	90.6	0.0	0.0	1.6	7.8	90.6	0.0	0.0	

Table 7 continued

	Early		Intermediates		Late	
	Transgressive segregants	Parent types	Transgressive segregants	Parent types	Transgressive segregants	Parent types
All	6.3	9.4	71.9	5.6	6.9	6.9
75% improved blue fruit			Fruit harvest			
Japanese/Kuril	25.0	25.0	31.3	9.4	9.4	3.1
Japanese/Russian	0.0	4.7	73.4	9.4	12.5	15.6
Kuril/Russian	3.1	6.3	90.6	0.0	0.0	0.0

Comparisons made by pairwise comparison using linear contrasts extracted from mixed regression models ( $p < 0.05$ )

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 were several more intermediate types 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 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.

#### Improved Kuril/Russian germplasm

The Kuril/Russian group reached bud break over a range of 9–13 days (Table 3), flowering onset over 20–30 days (Table 4) and fruit colouring/harvest over 18–21 days (Table 5). 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 (Fig. 3; Table 7). 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 proportion of intermediate types 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 intermediate types 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.

## 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 (Fig. 3; Table 7). 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 and 50% blue fruit, but considerably lower progressing toward harvest. 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.

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 to make intermediate types.

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 intermediate types with some dominance and overdominance of relatively later phenology. Compared to the other groups, the Kuril/Russian group showed a greater tendency to make intermediate types 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 latter 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.

#### Blueberry, raspberry and strawberry compared to improved germplasm

The blueberry cvs. 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 (Fig. 2; Table 3). 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). 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 5).

The earliest raspberry cv. 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 cvs. 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 cvs. 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 cvs., but the latest Japanese/Russian genotype reached 10 and 50% bud break as late as the earliest raspberry cv. 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 cvs. for initial harvest, final harvest in this crop stretching much later than any of the blue honeysuckle germplasm.

#### Conclusions

There was dominance and overdominance of intermediate Japanese over late Kuril phenology, being more evident at bud break than at bloom or harvest. 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 intermediate types 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 mainstream crops when higher average temperatures may permit expression of better fruit quality. 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 to enhance adaptation to temperate climates using Japanese/Kuril blue honeysuckle populations.

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