Genetic Diversity of Red Raspberry Varieties throughout the-World

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Additional index words. *Rubus idaeus*, fruit breeding, inbreeding, pedigree analysis

Abstract. Pedigrees of 137 red raspberry (*Rubus idaeus* L.) varieties released throughout the world since 1960 were used to calculate: 1) the genetic contribution of founding clones to these varieties; 2) genetic relatedness among them; and 3) their inbreeding coefficients. Fifty founding clones contributed to the pedigrees of these varieties with a mean genetic contribution ranging from <0.1% to 21%. Varieties were clustered according to the genetic contribution into groups strongly related to geographical origin. Varieties developed in the former USSR and derived from 'Novost Kuzmina' formed a distinct cluster. The remaining varieties were clustered in groups based mainly on whether they were of North American or European origin. Varieties were clustered also on the basis of Wright's coefficient of relationship—a measure of genetic relatedness. Cluster groups were related to their geographical origin and the varieties within the groups could be traced to similar intermediate parents. Inbreeding coefficients ranged from 0.0 to 0.625 and were related, in part, to the numbers of generations of controlled hybridization from common ancestors. The British group, with the largest number of generations of breeding, had a low mean inbreeding coefficient, indicating that inbreeding can be minimized with attention to the mating system. Strategies are suggested for maintaining and increasing the genetic diversity in the world's red raspberry breeding populations.

The red raspberry has been cultivated since before the fourth century. Since then, the plant has been genetically improved, first by the development of local varieties, and since about 1800, by deliberate hybridization (Jennings, 1988). To date, there have been three cycles of breeding: 1) many varieties were selected within *Rubus idaeus* subsp. *idaeus* and subsp. *strigosus* Michx. in the late 19th and early 20th centuries either from chance discoveries or from families of open-pollinated seedlings (Hedrick, 1925; Jennings, 1988); 2) some of these were used to produce *idaeus* × *strigosus* hybrid varieties; and 3) some of these hybrid varieties and some of the earlier chance discoveries were used to produce modern varieties (Jennings, 1988).

The result of this breeding strategy has been to produce varieties derived from very few parents, in particular 'Lloyd George'. Oydvin (1970) calculated that 69% of the varieties released between 1930 and 1970 were derived at least partially from 'Lloyd George'. Other varieties that have been important are 'Preussen' in Europe, 'Newman', 'Latham', 'Cuthbert', and 'Newburgh' in North America and 'Novost Kuzmina' in the former USSR (Daubeney, 1982; Jennings, 1988; Jennings et al., 1991; Oydvin, 1970).

The red raspberry was originally self-incompatible (Keep, 1968), but exploitation of a natural mutation at the incompatibility locus has enabled all modern varieties to be self-compat-

ible. This self-compatibility, however, encourages inbreeding, with losses in vigor, yield, and fruit size (Fejer and Spangelo, 1974).

Pedigree analysis has been used recently in other fruit crops to estimate the levels of inbreeding and genetic diversity of breeding populations (Hancock and Siefker, 1982; Lyrene, 1981; Scorza et al., 1985; Sjulín and Dale, 1987).

The purpose of this study was to use published red raspberry pedigrees to a) estimate the genetic diversity of the world raspberry varieties released since 1960, and b) use these results to suggest ways that the genetic diversity can be both maintained and increased. The pedigrees were used to calculate: a) the genetic contribution of older *Rubus* clones to the world's red raspberry varieties released since 1960, b) the degree of genetic relatedness among these varieties, and c) the level of inbreeding in these varieties.

Materials and Methods

The 137 raspberry varieties included in this study are named varieties of known parentage released throughout the world since 1960. Their pedigrees were obtained from various sources, including Brooks and Olmo (1971, 1972a, 1972b, 1973, 1974, 1975, 1978, 1982, 1983, 1984), Jennings (1988), published variety descriptions, and personal communications from raspberry breeders. Four varieties of unknown origin, 'Fallbrook', 'Rannyaya Sladkaya', 'Sweetbriar', 'Sparkling Gem' (*Rubus*

Received for publication 21 Jan. 1992. Accepted for publication 27 Apr. 1992. We thank C. Fear and V.H. Knight for contributions of unpublished pedigrees. The cost of publishing this paper was defrayed in part by the payment of page charges. Under postal regulations, this paper therefore must be hereby marked *advertisement* solely to indicate this fact.

Abbreviations: CR, coefficient of relationship; GC, genetic contributions.

phoenicolasius L.), and the Arctic raspberries were not included.

Calculations of the genetic contribution, the coefficient of relationship and inbreeding coefficients and cluster analyses, were based on the methods of Sjulín and Dale (1987).

Genetic contribution. The genetic contribution (GC) of a clone to a variety was calculated as: $GC = E (1/2)^n_{L \times x}$ where n is the number of generations in a pedigree pathway between the clone and the variety, and x is the total number of pathways between the clone and the variety. Three assumptions were made in GC calculations: 1) genotypes selected from open-pollinated populations were self-pollinated by the female parent; 2) where 'Loganberry' was found in a pedigree, the F_1 with red raspberry was considered to be diploid, with GC 50% 'Auginbaugh' blackberry, 25% 'Red Antwerp', and 25% red raspberry genotype; and 3) where *Rubus chamaemorus* L. was used, the F_1 was considered to be diploid with equal contributions from *R. chamaemorus* and the red raspberry. The first assumption may not always be correct, as 'Cuthbert' is thought to be a hybrid between 'Hudson River Antwerp' (Jennings, 1988) and *R. idaeus* subsp. *stigosus*, and Dale (unpublished data) has shown that up to 50% of selections from open-pollinated seed from small breeding plots of red raspberries can be hybrids. However, in the case of 'Cuthbert', which accounts for most of the 'Hudson River Antwerp' accessions, this will have 'little effect on the analyses, as either the self or the hybrid will have a unique germplasm. Pedigree pathways ended when a clone of unknown or disputed origin was encountered and that clone was classified as a "founding clone." A BASIC program was used with an IBM PC-AT microcomputer (Sjulín and Dale, 1987) to determine the percentage of GC of each founding clone to a given variety.

Varieties were grouped according to their GC using Ward's method (Ward, 1963). The GC of 21 founding clones that were present in the pedigrees of seven or more varieties were used as input variables. The remaining 29 founding clones were present in the pedigrees of five or fewer varieties. All varieties with identical or reciprocal parentage were represented by one of them. Clusters were merged until the decrease in the coefficient of determination caused by joining the clusters (semipartial R^2) exceeded 0.02.

Genetic relatedness. Genetic relatedness among varieties was estimated by coefficients of relationship (CR), which measure the probability that two individuals carry the same allele (Wright, 1922). CR were calculated from pedigrees as: $CR = 2 F_{xy}/d(1 + F_x)(1 + F_y)$, where F_{xy} is the inbreeding coefficient of offspring from the hypothetical mating between varieties x and y , and F_x and F_y are the inbreeding coefficients of varieties x and y , respectively (Hartl, 1980). Intermediate parent clones, as well as founding clones, shared in common between two varieties contributed to the CR.

The varieties were clustered by Ward's Method (Ward, 1963), and the CR were used as input variables. All varieties with identical or reciprocal parentage were represented by one of them, and CR were calculated for all possible combinations of hypothetical matings among these 124 varieties. A CR of 1.0 was used for self-matings. Clusters were merged until the semipartial R^2 exceeded 0.02.

Inbreeding. Inbreeding coefficients were calculated for each variety by Wright's Pedigree Method (Wright, 1922) SAS INBREED procedure (Barr, 1983). For the calculation of both the CR and inbreeding, genotypes selected from open-pollinated populations were considered to result from self-pollination, and

all F_1 s were considered to be diploid with equal contributions from each parent.

Results and Discussion

Genetic contribution. All 137 varieties of known parentage were derived from only 50 founding clones (Table 1). The mean GC of founding clones ranged from <0.1% to 21%. This range indicates that a restricted sample of the raspberry germplasm has been used for the world's red raspberry varieties. In comparison, the 134 North American strawberry (*Fragaria × ananassa* Duch.) varieties released over a similar period had 53 founding clones (Sjulín and Dale, 1987), and the 47 genetically improved highbush blueberry (*Vaccinium corymbosum* L.) varieties released up to 1982 originated from 17 founding clones (Hancock and Siefker, 1982).

Fourteen of the 15 founding clones with a mean GC > 1% were introduced in the 19th or early 20th centuries. All are red raspberries of either subsp. *idaeus* or subsp. *strigosus*. The 15th founding clone, 'Creston', is of unknown origin but was found in a commercial field in British Columbia. Fejer (1977) believed it to be at least 50% 'Lloyd George'.

Four founding clones occur in more than 90 pedigrees. These are 'Lloyd George', 'Hudson River Antwerp', 'English Globe', and 'Highland Hardy'. The latter three, however, are only found in two intermediate parents, 'Cuthbert' and 'Marlboro'; both are derived from 'Hudson River Antwerp', with 'Marlboro' also derived from 'English Globe' and 'Highland Hardy'.

'Lloyd George', which has a mean GC of 21%, is present in 79% of the varieties. This is more than the 69% that caused concern to Oydvin (1970). Indeed, if the Russian varieties are removed from the calculation, 'Lloyd George' is present in 87% of all European and American red raspberries.

Of the 21 founding clones occurring seven or more times in the pedigrees, the six with a mean GC <1% contain varieties of three species: a) *R. ursinus* Cham. et Schlecht 'Auginbaugh' is one parent of 'Loganberry', b) *R. chamaemorus* L., and c) *R. occidentalis* L. 'Cumberland'. Despite there being many named black raspberry varieties, 'Cumberland' is the only one that appears in the red raspberry pedigrees.

Of the remaining 25 founding clones, six species have been introduced for specific purposes. *Rubus parvifolius* Nutt. and *R. kunzeanus* Hemsl. have been introduced for heat tolerance (Overcash, 1973), *R. cockburneanus* Hemsl. for increased number of flowers (Knight et al., 1989), and *R. odoratus* L. for disease and pest resistance (Keep, 1989).

Cluster analysis, based on GC of the founding clones, sorted the varieties into 13 groups that were strongly related to geographic origin. All groups seem to be clustered according to a high GC of one or two founding clones. The greatest separation was between a small group of Russian varieties (cluster group 1) and the remainder of the varieties (Table 2; Fig. 1). All varieties in cluster group 1 have a high GC from 'Novost Kuzmina'.

The remaining 12 cluster groups were separated mainly on geographic origin, although the Russian varieties were included in several of the European groups.

Cluster group 2, the southern and central U.S. group, is characterized by approximately equal contributions from 'Ranere', 'Newman', and 'Lloyd George'. All the varieties in this group except one have a GC from 'Ranere' >13%. The GC from 'Ranere' came mostly through the intermediate parents 'Sunrise' and 'September', and those of 'Newman' through 'Newburgh', 'Taylor', and 'Marcy'. 'Malling Autumn Bliss' from the United

Table 1. Origin, frequency of occurrence, and GC of founding clones to the 137 world raspberry (*Rubus*) varieties.

Clone no.	Clone ^z	Origin	Frequency of occurrence	Mean GC (%)
1	Creston	British Columbia, Canada, about 1950	7	2
2	<i>R. idaeus</i> subsp. <i>strigosus</i> NY20990	New York, 1938	10	1
3	<i>R. chameamorus</i>	Unknown, before 1950	10	<1
4	<i>R. ursinus</i> Auginbaugh	California, 1881	13	1
5	Coutant	New York, before 1896	25	<1
6	King ^y	Virginia, 1892	20	3
7	Ranere	New Jersey, before 1912	25	3
8	Red Antwerp	England, before 1806	33	2
9	Newman ^x	Quebec, Canada, 1924	79	10
10	Herbert	Ontario, Canada, 1887	78	8
11	Hudson River Antwerp	England, before 1817	110	9
12	Lloyd George	England, 1919	108	22
13	English Globe	England, before 1869	90	2
14	Highland Hardy	New York, about 1870	90	5
15	Superlative ^w	England, about 1877	55	7
16	Pyne's Royal	England, 1913	39	4
17	Burnetholm	Scotland, before 1935	19	3
18	Baumforth A ^v	England, before 1865	14	<1
19	<i>R. occidentalis</i> Cumberland	Pennsylvania, before 1896	14	<1
20	Novost Kuzmina	NizhnyNovgorod, Russia, about 1890	12	4
21	Usanka	St. Petersburg, Russia, before 1950	7	2
22	Hornet	France, before 1858	6	<1
23	Devon	England, 1904	5	<1
24	Norfolk Giant	England, 1926	4	<1
25	Asker	Norway, before 1900	3	<1
26	<i>R. idaeus</i> subsp. <i>Strigosus</i>	Saskatchewan, Canada, before 1945	2	<1
27	Chey 62-17	Wyoming, 1962	2	<1
28	<i>R. pungens</i> Oldhami	Asia, before 1950	2	<1
29	<i>R. arcticus</i>	Finland, 1940	2	<1
30	<i>R. parvifolius</i>	Korea, before 1943	2	<0.1
31	<i>R. idaeus</i> subsp. <i>strigosus</i> NY21289	New York	2	<1
32	Chey 63-16	Wyoming, 1963	1	<1
33	Faistrup	Denmark, 1894	1	<1
34	<i>R. ×neglectus</i> Purple O.P.	Saskatchewan, Canada, before 1952	1	<1
35	<i>R. kunzeanus</i>	China, 1907	1	<0.1
36	<i>R. parvifolius</i>	Asia, before 1928	1	<1
37	<i>R. parvifolius</i>	China, about 1928	1	<1
38	<i>R. parvifolius</i>	Korea, before 1943	1	<0.1
39	<i>R. cockburneanus</i>	Asia, before 1950	1	<0.1
40	<i>R. odoratus</i>	Ontario, Canada, 1958	1	<0.1
41	<i>R. idaeus</i> subsp. <i>idaeus</i>	Finland, before 1950	1	<1
42	Phoenix	United States, before 1950	1	<1
43	Solge	Unknown, before 1950	1	<1
44	Shartashskaya	Yekaterinburg, Russia, before 1950	1	<1
45	Vislukha	Altai, Russia, before 1950	1	<1
46	Shpanka	Russia, before 1924	1	<1
47	<i>R. idaeus</i> subsp. <i>idaeus</i>	Altai, Russia, before 1950	1	<1
48	Reiter 323	California, before 1950	1	<1
49	Rose de Cote d'Or	France, before 1950	1	<1
50	Fertodi Hungaria ^a	Hungary, before 1970	1	<1

^zAll clones are *R. idaeus* varieties and numbered selections, unless indicated otherwise.

^y'Thompson' open-pollinated.

^xOpen-pollinated seedling of one of 'Cuthbert', 'Herbert', 'King', or 'Loudon'.

^wSynonymous with 'Northumberland Filbasket'.

^vDerived from 'Northumberland Filbasket'.

^a['Loganberry' × (*R. caesius* × 'Lloyd George') doubled] selfed (L. Kollanyi, personal communication).

Kingdom is included in this group, as its fall-bearing parent NY783 has 'September' contributing to three of its grandparents.

The largest and most geographically diverse group is cluster group 3. This contains North American varieties and their derivatives. It contains a high percentage GC of 'Newman' and

'Lloyd George' and either NY20990 or 'Herbert'. It contains all the North American fall-bearing varieties, except 'Heritage', and varieties from northern Europe, the former USSR, and Mexico.

All the American fall-bearing raspberries, except 'Joe Mello', trace their fall-bearing habits back to 'Heritage' or 'August Red'

Table 2. Cluster groups of the world's red raspberry varieties based on GC of founding clones.^z

Variety	GC (%) of founding clones ^y																					Other ^x
	Clone																					
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	
Cluster group 1 (Russian)																						
Prigorodnaya ^w	---	---	---	---	---	---	---	---	---	---	25	---	---	---	---	---	---	---	---	75	---	43(50)
Tenkovskaya Rannyaya	---	---	---	---	---	---	---	50	---	---	---	---	---	---	---	---	---	---	---	50	---	
Alenkaya	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	50	50	
Rannii Surpriz	---	---	---	---	---	---	---	---	---	---	---	25	---	---	---	---	---	---	---	50	25	
Samarskaya Ploynaya	---	---	---	---	---	---	---	---	---	---	6	---	6	13	25	---	---	---	---	50	---	
Odarka	---	---	---	13	---	---	---	6	---	---	14	13	2	3	---	---	---	---	---	50	---	
Meteor ^v	---	---	---	---	---	---	---	---	---	---	3	25	3	6	13	---	---	---	---	50	---	
Alyi parus	---	---	---	---	---	---	---	---	---	---	2	13	2	3	6	---	---	---	---	25	---	
Obilnaya	---	---	---	---	---	---	---	---	---	---	50	---	---	---	---	---	---	---	---	50	---	
Cluster group 2 (southern and central United States)																						
Lake Geneva	---	---	---	---	---	25	50	13	---	---	13	---	---	---	---	---	---	---	---	---	---	30(13) 38(13)
Liberty	---	---	---	---	---	13	25	6	25	25	6	---	---	---	---	---	---	---	---	---	---	
Southland	---	---	---	---	---	9	19	5	19	19	5	13	---	---	---	---	---	---	---	---	---	
Citadel	---	---	---	---	---	6	13	3	25	19	3	19	---	---	---	---	---	---	---	---	---	
Sentry	---	---	---	---	---	13	25	6	25	---	6	25	---	---	---	---	---	---	---	---	---	
Sentinel	---	---	---	---	---	13	25	6	13	13	6	25	---	---	---	---	---	---	---	---	---	
Reveille	---	---	---	---	3	6	37	3	13	6	4	25	1	2	---	---	---	---	---	---	---	
Scepter	---	---	---	---	---	---	25	---	37	---	---	37	---	---	---	---	---	---	---	---	---	
Cherokee ^u	---	---	---	---	---	---	25	---	25	13	---	25	---	---	---	---	---	---	---	---	22(13)	
Malling Autumn Bliss	---	---	---	---	1	---	16	---	15	2	1	22	1	2	3	2	6	7	2	---	24(3), 29(13), 31 (6)	
Cluster group 3 (North American and derivatives)																						
Nova	---	---	---	---	3	17	9	9	9	16	9	19	1	2	---	---	---	---	---	---	30(6)	
Joe Mello	---	---	---	---	---	3	---	2	13	13	8	13	---	---	---	---	---	---	---	---	48(50)	
Nordic	---	13	6	---	4	13	---	6	13	8	7	28	1	2	---	---	---	---	---	---	32(50) 27(50)	
Trailblazer	---	13	6	---	1	---	---	---	13	2	1	16	1	1	---	---	---	---	---	---		---
Pathfinder	---	13	6	---	1	---	---	---	13	2	1	16	1	1	---	---	---	---	---	---	---	
Fallred ⁱ	---	25	13	---	2	---	---	---	25	3	1	31	1	1	---	---	---	---	---	---	---	
Prestige	---	---	---	---	---	---	---	---	25	---	---	25	---	---	---	---	---	---	---	---	28(50)	
Fallgold	---	13	6	---	1	---	---	---	25	2	1	28	1	1	---	---	---	---	---	---	28(25)	
Redwing	---	13	6	---	1	---	---	---	28	5	13	34	1	1	---	---	---	---	---	---	22(13)	
Itasca	---	---	---	---	---	---	---	---	50	50	---	---	---	---	---	---	---	---	---	---		---
Royalty	---	---	---	---	3	---	---	---	25	31	1	13	1	2	---	---	---	---	25	---	---	
Festival	---	---	---	---	---	---	---	---	50	25	---	25	---	---	---	---	---	---	---	---	---	
Spolokh	---	---	---	---	---	---	---	---	37	37	---	13	---	---	---	13	---	---	---	---	---	
Titan	---	---	---	---	---	---	13	---	31	25	---	19	---	---	---	---	---	---	---	---	22(13)	
Dalnaya	---	---	---	6	---	---	3	3	37	25	8	13	2	3	---	---	---	---	---	---	---	
Jochems Roem	---	---	---	---	---	---	---	---	25	25	---	25	---	---	---	25	---	---	---	---	---	
Anita ^s	---	---	---	---	---	---	---	---	25	25	---	25	---	---	---	25	---	---	---	---	---	
Nootka	---	---	---	6	---	---	3	3	25	13	8	37	2	3	---	---	---	---	---	---	---	
Summit	---	6	3	---	1	---	6	---	31	16	6	30	1	1	---	---	---	---	---	---	---	
Watson (Ruby)	---	---	---	---	---	---	6	---	31	16	13	28	---	---	---	---	---	---	---	---	22(6)	
Himbo Queen	---	---	---	---	---	---	---	---	25	13	13	37	---	---	---	13	---	---	---	---	---	
Kirzhatch	---	---	---	6	---	---	3	3	25	13	8	25	2	3	---	13	---	---	---	---	---	
Amity	---	6	3	---	1	---	---	---	22	10	10	30	1	2	3	4	---	7	2	---	---	
Tulameen	---	---	---	3	---	---	2	2	16	9	5	31	2	4	5	3	9	2	2	---	23(6)	
Shopska Alena	---	---	---	---	---	---	---	---	25	25	3	25	3	6	13	---	---	---	---	---	---	
Ljulin	---	---	---	---	---	---	---	---	25	25	3	25	3	6	13	---	---	---	---	---	---	
Esenna Pozlata	---	---	---	---	---	---	---	---	25	25	3	25	3	6	13	---	---	---	---	---	---	
Chilcotin	---	---	---	---	---	6	---	3	25	25	16	25	---	---	---	---	---	---	---	---	---	
Hilton	---	---	---	---	---	---	---	---	25	25	---	25	---	---	---	---	---	---	---	---	22(25)	
Vene	---	---	---	---	---	---	---	---	25	25	---	25	---	---	---	---	---	---	---	---	25(25)	
Cluster group 4 (north Europe)																						
Norna ^f	---	---	---	---	---	---	---	---	---	---	6	50	6	13	25	---	---	---	---	---	---	
Balder	---	---	---	---	---	---	---	---	---	---	6	37	6	13	25	13	---	---	---	---	---	
Gradina ^a	---	---	---	---	---	---	---	---	13	13	3	37	3	6	13	13	---	---	---	---	---	
Spica	---	---	---	---	---	---	---	---	13	13	3	37	3	6	13	13	---	---	---	---	---	
Promiloy	---	---	---	---	---	---	---	---	13	13	3	37	3	6	13	13	---	---	---	---	---	
Sirius	---	---	---	---	---	---	---	---	13	13	3	50	3	6	13	---	---	---	---	---	---	
Zeva I	---	---	---	---	---	---	---	---	13	13	3	50	3	6	13	---	---	---	---	---	---	
Gevalo ^p	---	---	---	3	---	---	---	13	19	4	37	4	8	13	---	---	---	---	---	---	---	
Geloy	---	---	---	---	---	3	---	---	---	13	19	4	37	4	8	13	---	---	---	---	---	

continued

Table 2. *Continued.*

Variety	GC (%) of founding clones ^y																					Other ^x
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	
Sensation	---	---	---	---	13	---	---	---	---	25	3	50	3	6	---	---	---	---	---	---	---	25(50)
Perron's Red	---	6	3	---	2	---	---	---	---	6	4	1	52	1	1	---	---	---	---	---	---	
Veten ^o	---	---	---	---	---	---	---	---	---	---	---	50	---	---	---	---	---	---	---	---	---	
Nagrada	---	---	---	---	---	---	---	---	---	---	---	75	---	---	---	---	---	---	---	---	25	
Zeva Herbsternte	---	---	---	---	3	---	---	---	---	6	1	87	1	2	---	---	---	---	---	---	---	25(50)
Cluster group 5 (Superlative derivatives)	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	
Himbo Star	---	---	---	---	---	---	---	---	---	---	6	---	6	13	75	---	---	---	---	---	---	
Tchelyabinskaya	---	---	---	---	---	---	---	---	---	---	---	---	---	---	100	---	---	---	---	---	---	25(50)
Krupnoplodnaya	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	
Cluster group 6 (central Europe)	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	
Ruku	---	---	---	---	---	---	---	---	---	---	11	13	11	22	44	---	---	---	---	---	---	25(50)
Rucami	---	---	---	---	---	---	---	---	---	---	9	25	9	19	37	---	---	---	---	---	---	
Kaskad	---	---	---	---	---	---	---	---	---	---	9	25	9	19	37	---	---	---	---	---	---	
Zeva II	---	---	---	---	---	---	---	---	13	13	3	25	3	6	37	---	---	---	---	---	---	
Rutagro	---	---	---	---	2	---	---	---	6	9	8	19	8	16	31	---	---	---	---	---	---	25(50)
Rusilva	---	---	---	---	2	---	---	---	6	9	8	19	8	16	31	---	---	---	---	---	---	
Rumiloba	---	---	---	---	---	---	---	---	6	6	8	19	8	16	31	6	---	---	---	---	---	
Podgorina	---	---	---	---	---	25	---	13	---	---	16	---	3	6	38	---	---	---	---	---	---	
Vysokaya	---	---	---	---	---	---	---	---	---	---	6	---	6	13	25	---	---	---	---	---	---	44(50)
Yubileinaya	---	---	---	---	---	---	---	---	---	---	6	---	6	13	25	---	---	---	---	---	---	
Cluster group 7 (Great Britain)	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	46(50)
Malling Leo	---	---	---	---	---	---	---	---	---	---	2	13	2	3	7	7	50	13	3	---	---	
Glen Isla	---	---	---	---	---	---	---	---	---	---	2	34	2	4	8	9	25	3	13	---	---	
Glen Garry	---	---	---	---	---	---	---	---	4	4	2	32	2	4	7	11	25	3	2	---	---	
Malling Delight	---	---	---	---	---	---	---	---	3	3	1	39	1	2	4	14	31	2	---	---	---	23(6)
Malling Orion	---	---	---	---	---	---	---	---	---	---	4	22	4	7	14	22	25	3	---	---	---	
Glen Lyon	13	---	---	---	---	---	---	---	7	7	2	21	2	4	8	9	14	3	2	---	---	
Glen Clova	---	---	---	---	---	---	---	---	13	13	2	19	2	5	9	13	25	---	---	---	---	
Malling Joy	---	---	---	---	---	---	---	---	6	6	2	20	2	3	7	13	25	13	3	---	---	23(9)
Malling Augusta	---	---	---	---	---	---	---	---	4	4	2	23	2	4	8	14	19	10	3	---	---	
Malling Autumn	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	
Cascade	---	---	---	---	1	1	---	---	4	4	1	21	1	3	6	4	16	8	1	---	---	
Glen Prosen	---	---	---	---	---	---	---	---	6	6	2	24	2	5	10	5	19	4	3	---	---	24(3), 31(3)
Glen Moy	---	---	---	---	---	---	---	---	7	7	3	20	3	5	11	10	22	4	2	---	---	
Cluster group 8 (Pacific Northwest)	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	
Algonquin	25	---	---	---	---	---	---	---	6	6	16	31	3	6	---	6	---	---	---	---	---	
Chilliwak	25	---	---	3	---	3	2	3	6	---	13	22	2	3	3	3	13	---	---	---	---	23(13)
Centennial	25	---	---	---	---	---	---	---	6	6	26	16	1	2	3	3	13	---	---	---	---	
Comox	50	---	---	---	---	---	---	---	6	6	1	16	1	2	3	3	13	---	---	---	---	
Skeena	50	---	---	---	---	---	---	---	---	---	2	6	2	3	6	6	25	---	---	---	---	
Haida	50	---	---	---	---	---	---	---	13	13	---	13	---	---	---	13	---	---	---	---	---	33(13)
Cluster group 9 (Denmark)	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	
Zenith	---	---	---	---	---	---	---	---	---	---	3	---	3	6	---	75	---	---	---	---	---	
Futura	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	50	---	---	50	---	---	
Cluster group 10 (Latham derivatives)	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	47(50)
Earlibest ⁿ	---	---	---	---	---	50	---	25	---	---	25	---	---	---	---	---	---	---	---	---	---	
Redbrook	---	---	---	---	3	38	---	19	---	6	19	13	1	2	---	---	---	---	---	---	---	
Boyne ^m	---	---	---	---	6	25	---	13	---	13	14	25	2	3	---	---	---	---	---	---	---	
Cluster group 11 (northern United States and Russia)	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	26(50)
Frazer	---	---	---	---	---	25	---	13	---	---	44	---	6	13	---	---	---	---	---	---	---	
Zorenka Altaya	---	---	---	---	---	---	---	---	---	---	31	---	6	13	---	---	---	---	---	---	---	
Honeyqueen	---	---	---	---	---	---	---	---	---	---	31	---	6	13	---	---	---	---	---	---	---	
Lazarevskaya	---	---	---	6	---	---	3	3	13	---	11	25	5	9	13	13	---	---	---	---	---	49(50)
Sputnitsa ^l	---	---	---	13	---	---	6	6	---	---	19	25	6	13	13	---	---	---	---	---	---	
Meco	---	---	---	---	---	---	---	---	6	6	25	13	---	---	---	---	---	---	---	---	---	
Fertodi Zamos	---	---	---	---	---	---	---	---	---	---	16	25	3	6	---	---	---	---	---	---	---	
Fertodi Ketszertermo	---	---	---	---	---	---	---	6	---	---	34	25	3	6	---	---	---	---	---	---	---	50(50)
	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	
	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	22(25)
	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	

continued

Table 2. *Continued.*

Variety		GC (%) of founding clones ^y																					Other ^x
		Clone																					
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	
Novost Mikholatchuka	---	---	---	13	---	---	---	13	---	---	28	25	3	6	---	---	---	---	---	---	---		
Fairview	---	---	---	---	---	---	---	---	13	13	25	25	---	---	---	25	---	---	---	---	---		
Meeker	---	---	---	---	---	---	---	---	13	13	50	25	---	---	---	---	---	---	---	---	---		
Avon	---	---	---	---	---	---	---	---	13	13	50	13	---	---	---	13	---	---	---	---	---		
Heritage ^k	---	---	---	---	---	---	---	---	31	6	25	37	---	---	---	---	---	---	---	---	---		
Matsqui	---	---	---	6	---	6	3	6	13	---	23	37	2	3	---	---	---	---	---	---	---		
Wawi	---	---	---	---	---	---	---	---	13	13	25	50	---	---	---	---	---	---	---	---	---		
Cluster group 12 (Russian-Usanka derivatives)																							
Amurchanka	---	---	---	---	---	---	---	---	---	---	13	25	13	25	---	---	---	---	---	---	25		
Dotch Amurchanki	---	---	---	---	---	---	---	---	---	---	13	25	13	25	---	---	---	---	---	---	25		
Barnaulskaya	---	---	---	---	---	---	---	---	---	---	31	---	6	13	---	---	---	---	---	---	50		
Vera	---	---	---	---	---	---	---	---	---	---	19	---	6	13	13	---	---	---	---	25	25		
Cluster group 13 (unique)																							
Novost Krasnoyarska	---	---	---	50	---	---	---	25	---	---	6	---	6	13	---	---	---	---	---	---	---		
Malling Admiral	---	---	---	---	---	---	---	---	6	6	2	6	2	3	6	6	13	---	---	---	24(50)		
Dormanred	---	---	---	---	---	---	---	---	---	---	13	---	---	---	---	---	---	---	---	---	35(13), 36(75)		
Redman	---	---	---	---	---	---	---	---	---	---	16	---	3	6	---	---	---	---	---	---	26(25), 34(50)		
Ville	---	---	---	13	---	---	6	6	---	---	---	---	3	6	---	---	---	---	---	---	41(50)		
Alma Atinskaya	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	42(100)		
Dotch Vislukha	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	45(100)		

^xCluster analysis (Ward's hierarchical method) based on GC of founding clones nos. 1–21.

^ySee Table 1 for names of founding clones.

^zPercent GC in parentheses; number preceding parentheses is founding clones no. (see Table 1).

^aSibling: 'Novokitayevskaya'.

^bSibling: 'Bryanskaya'.

^cSibling: 'Pocahontas'.

^dSibling: 'Augustred'.

^eSibling: 'Gina'.

^fSibling: 'Ralitsa'. 'Granat' added after analysis.

^gSibling: 'Krupna Dvoroda'.

^hSibling: 'Trajilo'.

ⁱSibling: 'Synga'.

^jSibling: 'Ott's Pennridge'.

^kSibling: 'Killarney'.

^lSibling: 'Skromnitsa'.

^mSport: 'Kiwigold'.

and its sib 'NH56-1'. All three have 'Durham' as the fall-bearing ancestor. Both *R. chameamorus* L. and NY20990 are ancestors of 'August Red' and 'NH56-1'. The fall-bearing pedigree of 'Joe Mello' is unknown.

With the exception of 'Prestige', all the summer-bearing varieties in this group are closely related to 'Newburgh' ('Newman' × 'Herbert'). 'Itasca' is 'Newburgh' selfed; 'Spolokh', 'Dalanya', 'Shopska Elena', 'Ljulin', 'Chilcotin', 'Vene', and 'Hilton' all had 'Newburgh' as one parent. 'Festival' had 'Mus-koka', a sib of 'Newburgh', as one parent. All the other summer-bearing varieties in this group, except 'Tulameen' and 'Nova', had 'Newburgh' as at least one grandparent, often with 'Malling Promise' and 'Malling Exploit' as the intermediate parent. In 'Tulameen', 'Newburgh' is found in the pedigrees of both 'Nootka' and 'Glen Prosen', and in 'Nova', 'Newburgh' is present in the pedigree of 'Southland'.

Cluster group 4, the north European group, includes the two North American varieties (Sensation) and (Perron's Red). This group is characterized by a high percent GC from 'Lloyd George'. Intermediate parents in this group are 'Preussen' and 'Newburgh'. 'Norna' and 'Ralitsa' are sibs from the cross 'Preussen' × 'Lloyd George'. Eight other varieties in this group have other

varieties from this cross as one of their parents. 'Newburgh' enters the pedigrees mainly through 'Malling Exploit', 'Malling Promise', and 'Willamette'.

Cluster group 5 contains two 'Superlative' derivatives. 'Superlative' contributes at least 75% of the GC to both varieties.

In cluster group 6, the central European group, all varieties except 'Zeva II' and 'Podgorina' have either 'Preussen' or its sib '4A' as one parent. The two exceptions have 'Rote Wadenswil' ('Preussen' × 'Superlative') as one parent. Also, the five German varieties and 'Kaskad' have varieties from the cross 'Preussen' × 'Lloyd George' as one grandparent. This gives the high percent contribution of 'Superlative' to this group.

Cluster group 7, the British group, contains all the British varieties except 'Malling Autumn Bliss' and 'Malling Admiral'. All have a complex pedigree that, in some cases, can be traced back 13 generations. All have seven founding clones ('Lloyd George', 'Burnetholm', 'Pyne's Royal', 'Superlative', 'Hudson River Antwerp', 'English Globe', and 'Highland Hardy') with high percent GC from 'Lloyd George' and 'Burnetholm'.

Cluster group 8, the Pacific Northwest group, contains six varieties that are closely related and are essentially hybrids between 'Creston' and British germplasm. 'Chilliwick', 'Centen-

Fig. 1. Cluster dendrogram of the world's red raspberry varieties based on GC of founding clones, using Ward's hierarchical method. Vertical bars indicate relative numbers of varieties in each group. Varieties composing cluster groups are listed in Table 2.

nial', and 'Comox' have 'Skeena' as one parent, and 'Algonquin' has 'Haida' as one parent. 'Skeena' and 'Haida' are hybrids of 'Creston' with British selections.

The two Danish varieties in cluster group 9 have 'Pyne's Royal' as at least one parent.

Cluster group 10, 'Latham' derivatives, contains five varieties. 'Earlibest' and 'Ott's Pennridge' are 'Latham' selfed, and 'Redbrook' is three-quarters derived from 'Chief', which is also 'Latham' selfed. 'Boyne' and 'Killarney' have 'Chief' as one parent.

Cluster group 11, the northern group of varieties from North America, the former USSR, France, and Hungary, contains varieties with a high GC from 'Lloyd George' and 'Hudson River Antwerp'. The 'Hudson River Antwerp' contribution is derived through the intermediate parent 'Cuthbert'. 'Viking' ('Cuthbert' × 'Marlboro') is either one parent or a grandparent of half the varieties in this group: 'Fertodi Zamos', 'Frazer', 'Honeyqueen', 'Lazarevskaya', 'Matsqui', 'Skromnitsa', 'Sputnitsa', and 'Zorenka Altaya'. 'Washington', another offspring of 'Cuthbert', is one parent of 'Fairview', 'Matsqui', and 'Wawi'.

Cluster group 12 contains four Russian varieties related to 'Usanka' and 'Marlboro'.

Cluster group 13, the unique group, contains those varieties with at least half GC from rare or unique founding clones.

Genetic relatedness. The CR values for matings between individual varieties usually did not deviate markedly from the mean coefficient relationship for matings with or between their respective cluster groups (data not presented). Therefore, only

the mean CR within or between cluster groups are presented (Table 3). The varieties included in each cluster group are listed in Table 4.

Cluster analysis based on CR (Table 4; Fig. 2) generally support relationships between varieties described by their GC (Table 2; Fig. 1). There are differences between the two cluster analyses because methodologies differ. When clusters are based on GC, the founding clones are the criteria used and intermediate parents are irrelevant. When clusters are based on CR, intermediate parents become more important.

Groups 1 and 2 are distinct groups with high CR within each group and low coefficients with other groups. Group 3 has low CR both within the group and with other groups. Groups 4-6 have high CR between these groups and with groups 9 and 10. Groups 7-10 are less distinct and have high levels of relationship with each other.

Cluster group 1 is composed of varieties that originated in north-central North America. All of the varieties have a high percentage of 'Latham' or 'Chief' ('Latham' selfed).

Cluster group 2, the Russian group, is identical to the Russian group from the analysis of the GC, except for 'Odarka'. It is not closely related to any other group. All its varieties are closely related to 'Novost Kuzmina'.

Cluster group 3 is the unique group. Two varieties, 'Alma Atinskaya' and 'Dotch Visluka' had a CR of 0 with all varieties. Both are derived directly from clones of unknown ancestry. This group had low CR within the group and with all other groups.

Cluster group 4, 'Loganberry'-'Marlboro' derivatives, is composed of varieties with 'Loganberry' in their ancestry. These varieties were derived from 'Loganberry' through 'Ottawa' or 'Texas'. The other five varieties in this group have 'Marlboro' and/or 'Cuthbert' in their derivation.

Cluster group 5, the 'Preussen'-'Superlative' group, contains group 6 of the analysis of the GC with both varieties from group 5 plus 'Norna' and 'Balder' of group 4. Varieties in this group are related to 'Preussen' ('Superlative' × 'Marlboro') or 'Superlative'. This group has high CR with cluster group 10.

Cluster group 6 contains all of the British varieties and some Pacific Northwest varieties derived from British material. All of the varieties have 'Burnetholm' in their ancestry and most also contain 'Cumberland'.

Cluster group 7, the North American fall-fruited group, contains fall-fruited varieties and some related summer-fruited varieties. Nine of the 17 varieties in this group have NH-R7 varieties in their pedigrees. The remaining eight varieties are included in this group because they share common ancestry with this group of nine. 'Fallgold' has NH-R7 as one parent and 'Taylor' × *R. pungens oldhamii* Mig. hybrid as the other parent. This is one of the parents of 'Prestige', and, as a result, 'Prestige' is included through its relationship to 'Fallgold'. 'Heritage', 'Scepter', and NH-R7 all have 'Durham' as a parent. 'Watson' (Ruby) has 'Heritage' as one parent. The remaining four varieties all have 50% 'Lloyd George' or more in their pedigrees. Varieties in this group have high CR with groups 8-10.

Cluster group 8, the 'Newburgh'-'Sunrise' group, is composed primarily of varieties from the eastern United States. Fourteen of the 17 varieties in this group have at least 25% 'Newburgh' in their parentage. Four of these 14 also have at least 25% 'Sunrise'. The three varieties that do not contain 25% 'Newburgh' ('Nova', 'Reveille', and 'Sentry') all have at least 25% 'Sunrise'. 'Festival' is 50% 'Muskoka', a sib of 'Newburgh', and therefore is included in this group.

Cluster group 9, the 'Malling Exploit'-'Malling Promise'

Table 3. Mean CR for matings of raspberry varieties within and between cluster groups.^z

Cluster group		Cluster group no.									
No.	Name	1	2	3	4	5	6	7	8	9	10
1	Latham	0.438									
2	Novost Kuzmina	0.039	0.270								
3	Unique	0.054	0.033	0.060							
4	Loganberry-Marlboro	0.101	0.085	0.071	0.174						
5	Preussen-Superlative	0.065	0.075	0.047	0.119	0.284					
6	British	0.033	0.045	0.026	0.079	0.101	0.198				
7	Fall Fruiting	0.066	0.055	0.011	0.094	0.065	0.089	0.240			
8	Newburgh-Sunrise	0.104	0.029	0.010	0.065	0.047	0.077	0.143	0.234		
9	Malling Exploit-Malling Promise	0.077	0.047	0.048	0.127	0.074	0.134	0.148	0.181	0.255	
10	Lloyd George x Preussen	0.047	0.077	0.027	0.126	0.196	0.146	0.168	0.187	0.218	0.306

^zAll possible matings, self-matings excluded. Varieties composing cluster groups are listed in Table 4.

group, includes 13 varieties that originated in diverse locations. Seven of the 13 varieties have either 'Malling Exploit' or its sib, 'Malling Promise', in their pedigrees. 'Kirzhatch' is 50% 'Malling Promise' and 50% 'Carnival'. 'Dalnaya', 'Nootka', and 'Tulameen' all have >25% 'Carnival' and form a subgroup within this cluster. 'Nootka', 'Meeker', and 'Wawi' all have 'Willamette' as one parent.

Cluster group 10, the 'Lloyd George' × 'Preussen' group, has European and Russian varieties derived from one of five clones from the cross of 'Lloyd George' × 'Preussen' or its reciprocal. Nine of the 11 varieties have No. 185, 'Paul Camenzind', 'Klon II Munchenberg', 'Rubin', or 'Schoenmann' in their pedigrees. 'Spica' and 'Zeva II' are both 'Preussen' derivatives crossed with 'Willamette' and are included in this group based on their relationship to 'Sirius' and 'Zeva I'. This group has a high CR with group 5, the 'Preussen-Superlative' group. 'Norna' is another variety from the cross of 'Preussen' × 'Lloyd George' but is in group 5 with varieties with a higher proportion of 'Superlative', rather than with those in group 10.

Levels of inbreeding. Inbreeding coefficients of varieties ranged from 0.0 for 42 varieties to 0.625 for 'Himbo Star', with 12 varieties having an inbreeding coefficient of 0.5 (Table 4). The inbreeding coefficients are subject to the accuracy of the pedigree records. If more complete records were available, some of the founding clones would be identified as being related. Because these records are lacking, the founding clones are assumed to be unrelated, and, as a result, the estimate of the inbreeding coefficient may be too low. However, open-pollinated seedlings were assumed to be the result of self pollination. In the case where open-pollinated seedlings were actually hybrids, this assumption may overestimate the inbreeding coefficient.

The British and Pacific Northwest varieties in cluster group 6 of the genetic relatedness analysis have the longest breeding history, but this group has one of the lowest inbreeding coefficients (0.076). This result indicates that inbreeding can be minimized with attention to the mating system.

Even where the inbreeding coefficients are, on average, high, it does not necessarily mean that there is a high degree of homozygosity. Shaw (1991) commented on the high inbreeding coefficients calculated by Sjulín and Dale (1987) for strawberry. He thought that their estimates were high because 1) breeding populations were maintained with a larger genetic base, and 2) in California, there was no correlation between inbreeding coefficients and the performance variables for several breeding lines.

Also, in red raspberry the heterozygote appears to have a selective advantage (Jennings, 1967, 1972).

Maintaining and increasing genetic diversity. Four strategies can be and are being adopted by red raspberry breeders throughout the world to maintain or increase genetic diversity. These are a) increase the number of parents per generation, combined with a controlled system of mating; b) introduce partly or completely unrelated germplasm from improved sources of red raspberry; c) introduce germplasm from wild *R. idaeus* subsp. *idaeus* or *stigosus*; and d) introduce unimproved germplasm from other species of the subgenus *idaebatus*.

Increasing the number of parents per generation reduces the rate of inbreeding (Li, 1955) and minimizes the loss of genetic diversity by random genetic drift (Allard, 1960). Random genetic drift will increase the actual level of inbreeding above that estimated in Table 4 (Hartl, 1980). When a controlled system of mating is practiced, in which the least-related parents of each generation are intercrossed, the rate of inbreeding will be half that of a random-mating population (Li, 1955).

Genetic diversity can be increased by introduction of partially or unrelated *R. idaeus* improved germplasm. The pedigree analysis indicates that genetic diversity in European and North American varieties can be increased if the Russian varieties derived from 'Novost Kuzmina' are crossed with them. Also, the crosses between European and North American varieties will continue to increase the genetic diversity within the resulting varieties.

Genetic diversity can also be increased by using wild germplasm from *R. idaeus* subsp. *idaeus* and *strigosus*. Although subsp. *idaeus* has been studied by several workers (Haskell, 1960; Jennings, 1964; Keep, 1972; Misic and Tesovic, 1973; Rousi, 1965; Rozanova, 1939), very few traits were considered to be useful in raspberry breeding. In subsp. *strigosus*, however, useful characters have been identified from studies of a relatively small germplasm base (Daubeny, 1972, 1980; Dorsey, 1921; Van Adrichem, 1972; Vrain and Daubeny, 1986). Within this subspecies, hardiness, large fruit size, aphid resistance, and resistance to the nematode *Pratylenchus penetrans* (Cobb) Fil. & S. Stek. and cane diseases (H.A. Daubeny, personal communication) have been identified.

The subgenus *idaebatus* Focke has more than 200 species that can be used to increase the genetic diversity within red raspberry. Many have been used as donors to improve breeding, mostly for resistance to pests and diseases (Jennings, 1988), although few have so far contributed to named varieties. *Rubus*

Table 4. Origin and inbreeding coefficients (F) of raspberry cultivars grouped by CR cluster analysis.

Variety	Origin	F
Group 1 (Latham)		
Boyne	Manitoba, Canada, 1960	0.004
Killarney	Manitoba, Canada, 1961	
Earlibest	Minnesota, 1960	0.500
Ott's Pennridge	Pennsylvania, 1965	
Frazer	Saskatchewan, Canada, 1960	0.109
Lake Geneva	Wisconsin, 1960	0.000
Redbrook	Alberta, Canada, 1983	0.377
Group 1 mean		0.198
Group 2 (Novost Kuzmina)		
Alenkaya	Altai, Russia, 1965	0.000
Alyi Parus	Bryansk, Russia, 1987	0.000
Meteor	Bryansk, Russia, 1987	0.000
Bryanskaya	Bryansk, Russia, 1987	
Obilnaya	Nizhniynovgorod, Russia, 1965	0.000
Prigorodnaya		
Novokitayevskaya	Kiev, Ukraine, 1974	0.250
Rannii Surpriz	Samara, Russia, 1986	0.000
Samarskaya		
Plotnaya	Sumara, Russia, 1986	0.000
Tenkovskaya		
Rannyaya	Tatar, Russia, 1974	0.000
Group 2 mean		0.031
Group 3 (unique)		
Alma Atinskaya	Kazakhstan, 1973	0.500
Barnaulskaya	Altai, Russia, 1961	0.000
Dormanred	Mississippi, 1972	0.000
Dotch Vislukhi	Altai, Russia, 1985	0.500
Futura	Denmark, 1985	0.000
Honeyqueen	Alberta, Canada, 1966	0.500
Redman	Saskatchewan, Canada, 1961	0.000
Vera	Altai, USSR, 1989	0.039
Ville	Finland, 1988	0.000
Zenith	Denmark, 1985	0.250
Zorenka Altaya	Altai, USSR, 1990	0.500
Group 3 mean		0.208
Group 4 (Loganberry--Marlboro)		
Amurchanka	Amur region, Russia, 1988	0.000
Dotch Amurchanki	Amur region, Russia, 1989	0.500
Ferdoti Ketszer-termo	Hungary, 1988	0.000
Ferdoti Zumatos	Hungary, 1986	0.000
Lazarevskaya	Moscow, Russia, 1988	0.051
Matsqui	British Columbia, Canada, 1961	0.099
Meco	France, 1987	0.000
Novost Krasnoyarska	Krasnoyarsk, Russia, 1974	0.000
Novost Mikho-laichuka	Ukraine, 1987	0.031
Odarka	Ukraine, 1988	0.000
Sputnitsa	Bryansk, Russia, 1983	0.039
Skromnitsa	Bryansk, Russia, 1983	
Group 4 mean		0.065
Group 5 (Preussen-Superlative)		
Balder	Norway, 1988	0.188
Himbo Star	Switzerland	0.625
Kaskad	Bryansk, Russia, 1990	0.250
Norna	Norway, 1961	0.000
Ralitsa	Bulgaria, 1980	
Granat	Czechoslovakia, 1982	
Podgorina	Yugoslavia, 1988	0.008
Rucami	Germany, 1980	0.125
Ruku	Germany, 1980	0.313
Rumiloba	Germany, 1980	0.063
Rusilva	Germany, 1980	0.201
Rutagro	Germany, 1980	0.070

continued

Table 4. continued.

Variety	Origin	F
Tchelyabinskaya		
Krupnoplodnaya	Tchelyabinsk, Russia, 1965	0.500
Vysokaya	Yekaterinburg, Russia, 1979	0.000
Yubileinaya	Tatar, USSR, 1974	0.000
Group 5 mean		0.180
Group 6 (British)		
Malling Autumn		
Bliss	England, 1983	0.027
Malling Autumn		
Cascade	England, 1990	0.161
Centennial	Washington, 1989	0.012
Chilliwack	British Columbia, Canada, 1986	0.015
Comox	British Columbia, Canada, 1986	0.133
Glen Clova	Scotland, 1969	0.047
Glen Garry	Scotland, 1989	0.100
Glen Isla	Scotland, 1974	0.047
Glen Lyon	Scotland, 1989	0.152
Glen Moy	Scotland, 1981	0.172
Glen Prosen	Scotland, 1981	0.106
Malling Admiral	England, 1971	0.000
Malling Augusta	England, 1989	0.139
Malling Delight	England, 1973	0.129
Malling Joy	England, 1980	0.115
Malling Leo	England, 1976	0.000
Malling Orion	England, 1971	0.016
Skeena	British Columbia, Canada, 1977	0.000
Group 6 mean		0.076
Group 7 (fall-fruited)		
Amity	Oregon, 1984	0.081
Fallgold	New Hampshire, 1967	0.117
Fallred	New Hampshire, 1964	0.070
August Red	New Hampshire, 1973	
Heritage	New York, 1969	0.094
Kiwigold	New Zealand, 1988	
Nagrada	Nizhniynovgorod, Russia, 1973	0.250
Nordic	Minnesota, 1987	0.063
Pathfinder	Wyoming, 1976	0.000
Perron's Red	Quebec, Canada, 1987	0.074
Prestige	New Hampshire, 1979	0.250
Redwing	Minnesota, 1986	0.177
Septer	Maryland, 1966	0.125
Sensation	Illinois, 1974	0.500
Summit	Oregon, 1989	0.236
Trailblazer	Wyoming, 1976	0.000
Veten	Norway, 1961	0.000
Synga	Norway, 1961	
Watson (Ruby)	New York, 1988	0.107
Zeva Herbstente	Switzerland, 1963	0.500
Group 7 mean		0.156
Group 8 (Newburg--Sunrise)		
Cherokee	Virginia, 1972	0.063
Pocahontas	Virginia, 1972	
Chilcotin	British Columbia, Canada, 1977	0.000
Citadel	Maryland, 1966	0.086
Festival	Ontario, Canada, 1972	0.125
Hilton	New York, 1965	0.000
Itasca	Minnesota, 1965	0.500
Joe Mello	California	0.000
Liberty	Iowa, 1976	0.000
Nova	Nova Scotia, Canada, 1981	0.075
Reveille	Maryland, 1966	0.094
Royalty	New York, 1982	0.141
Sentinel	Maryland, 1966	0.000
Sentry	Maryland, 1966	0.000
Southland	North Carolina, 1968	0.094
Spolokh	Moscow, Russia, 1988	0.250
Titan	New York, 1986	0.156
Vene	Norway, 1987	0.000

continued

Table 4. continued.

Variety	Origin	F
Group 8 mean		0.093
Group 9 (Malling Exploit-Malling Promise)		
Agonquin	British Columbia, Canada, 1990	0.031
Anita	Mexico, 1989	0.500
Gina	Mexico, 1989	
Avon	Nova Scotia, 1967	0.000
Dalnaya	Moscow, Russia, 1987	0.063
Fairview	Oregon, 1961	0.000
Haida	British Columbia, 1973	0.000
Himbo Queen	Switzerland	0.094
Jochems Roem	Netherlands, 1966	0.500
Kirzhatch	Moscow, Russia, 1985	0.063
Meeker	Washington, 1967	0.000
Nootka	British Columbia, Canada, 1977	0.094
Tulameen	British Columbia, 1990	0.069
Wawi	France, 1987	0.125
Group 9 mean		0.118
Group 10 (Lloyd George x Preussen)		
Ljulin	Bulgaria, 1982	0.000
Krupna Dvoroda	Yugoslavia, 1975	0.063
Gradina	Yugoslavia, 1975	
Esenna Pozlata	Bulgaria, 1985	0.250
Geloy	Germany, 1963	0.070
Gevalo	Germany, 1963	0.070
Tragilo	Germany, 1963	
Promiloy	Germany, 1963	0.063
Shopska Alena	Bulgaria, 1985	0.000
Sirius	Netherlands, 1973	0.125
Spica	Netherlands, 1973	0.063
Zeva I	Switzerland, 1960	0.125
Zeva II	Switzerland, 1960	0.000
Group 10 mean		0.075
Overall Mean		0.118

*Cluster analysis (Ward's hierarchical method) based on CR for all possible combinations of matings, full-sib matings excluded.

Fig. 2. Cluster dendrogram of the world's red raspberry varieties based on CR, using Ward's hierarchical method. Varieties composing cluster groups are listed in Table 4. Vertical bars indicate relative numbers of varieties in each cluster group.

occidentalis has been used as a donor of fruit firmness and resistance to all strains of *Amphorophora idaei* Börn (Keep and Knight, 1968). However, to date, germplasm from only 'Cumberland' has been used in developing red raspberry varieties, despite the species being completely interfertile with *R. idaeus*. *Rubus parvifolius* and *R. kunzeanus* have been used to develop varieties for warm climates (Jennings, 1988), *R. cockburneanus* for late-season and many-flowered laterals (Knight, et al., 1989), *R. spectabilis* Pursh. for earliness (Knight, 1991), and *R. arcticus* L. for flavor (Hiirsalmi, 1989). Many species, both within subgenus *idaebatus* and in other subgenera, have been reported to carry other traits, including resistance to all major fungal diseases and insect pests (Keep, 1989). However, the F_1 hybrids of these species with *R. idaeus* are often partially or completely sterile, which necessitates several generations of backcrossing to regain fertility (Keep and Knight, 1968).

To increase genetic diversity, a well-planned approach through recurrent selection is needed. This topic was discussed in Sjulín and Dale (1987) in relation to increased genetic diversity in the strawberry. Their discussion concluded that a recurrent selection system would require more generations of selection than a backcross system of mating but would allow for continued improvement of multiple traits for many generations.

Any of the four strategies outlined here can be used to maintain or increase genetic diversity within red raspberry. The first

two strategies will maintain the genetic diversity in the short term, but the latter two are required to maintain long-term improvement in red raspberries.

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