Maternal and Paternal Influences on Crumbly Fruit of 'Centennial' Red Raspberry

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Abstract. A crumbly fruited clone of 'Centennial' red raspberry (*Rubus idaeus* L.) had fewer drupelets per fruit and smaller fruit than normal-fruited 'Centennial'. Although there was more abortive pollen in the crumbly clone of 'Centennial', there was no difference in drupelet set between the two 'Centennial' clones when used as paternal parents. Thus, in 'Centennial', the mechanism causing crumbly fruit was primarily a maternal effect. There was no evidence of disease as a cause of the crumbly fruited 'Centennial' clone and observations were consistent with a somatic mutation.

Crumbly fruit occurs in some cultivars of red raspberry. Crumbly fruit have fewer drupelets, resulting in fruits that may crumble when picked due to poor drupelet adhesion. This condition has been reported in many cultivars, including 'Sumner' (Daubeney et al., 1967), 'Malling Promise', 'Norfolk

Giant', 'Mailing Jewel', 'Lloyd George', and 'Latham' (Jennings, 1967). There are several known causes for crumbly fruit. Some cultivars and selections have reduced drupelet set when self-pollinated, possibly due to partial self-incompatibility (Daubeney, 1971). Unidentified viruses were thought to cause crumbly fruit in 'Mailing Promise' and 'Norfolk Giant' (Jennings, 1967). Pollination by raspberry bushy dwarf virus (RBDV)-infected pollen resulted in crumbly fruit (Murant et al., 1974), and RBDV-infected plants produced crumbly fruit even when pollinated by virus-free pollen (Daubeney et al., 1978). Tomato ringspot virus (TomRSV) also may cause crumbly fruit (Daubeney et al., 1970). Crumbly fruit of 'Mailing Jewel' and 'Latham' was thought to result from mutation of a dominant allele at a heterozygous locus, resulting in homozygosity for reduced fertility (Jennings, 1967). In 'Sumner', crumbly fruit was thought to result from mutations at

two loci (Daubeney et al., 1967).

In grower trials of 'Centennial', crumbly fruit was observed in some plants (Moore et al., 1990). Crumbly fruited plants were tested for viruses by mechanical transmission to *Chenopodium quinoa*, double-stranded RNA analysis, and ELISA. These tests would detect tobacco streak virus, RBDV, TomRSV, and an ilar-like virus. Crumbly fruit in 'Centennial' was not associated with any of these viruses (Martin, 1988). In the same survey, crumbly fruit was found in 'Skeena' that was not associated with viruses. 'Skeena' is the male parent of 'Centennial'. All of the crumbly fruited plants were from one micropropagated source and a somatic mutation was suspected.

Preliminary studies in 1987 indicated that crumbly 'Centennial' had a higher proportion of abortive pollen, as determined by acetocarmine staining, compared with normal 'Centennial' (54% vs. 7% abortive pollen). This difference suggested a paternal contribution to crumbly fruit in 'Centennial'. The research reported here was initiated to study the relative contributions of maternal and paternal effects in crumbly fruited 'Centennial'.

Crumbly and normal-fruited plants of 'Centennial' in a commercial field and 'Willamette' and 'Chilcotin' plants in a separate commercial field were used in the study. There was no evidence of crumbly fruit in the normal 'Centennial', 'Willamette', or 'Chilcotin' plants. Both fields were located near Puyallup, Wash., within 10 km of each other. One hill of each clone was used for each replication, and all possible pollinations among the four clones were made, including selfs (16 crosses per replication). Four replications totalling 64 pollinations were made. Flower buds were emasculated and enclosed in pollination bags using standard pollination techniques. Beginning 9 June 1988, flowers were pollinated at 2-day intervals up to seven

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Table 1. Percent abortive pollen of four red raspberry clones at Puyallup, Wash., in 1988.^z

Clone	Abortive pollen (%)
Crumbly Centennial	55.2 a
Normal Centennial	19.6 c
Chilcotin	40.9 b
Willamette	37.9 b

^zEach mean is based on counts of 8000 pollen grains from 20 flowers. Mean separations by Duncan's multiple range test, $P = 0.05$.

Table 2. Mean squares from analysis of maternal and paternal effects on raspberry fruit development at Puyallup, Wash., in 1988.^z

Source of variation	df	Fruit wt	Drupelet no.
Replication	3	0.89	369
Maternal	3	8.68**	2353**
Paternal	3	10.84**	3967**
Maternal × paternal	9	1.26*	333*
Error	45	0.46	134

^z***F test of mean-square ratios significant at $P = 0.05$ or 0.01 .

times using fresh flowers for pollen. After fruit set, open-pollinated flowers were enclosed in pollination bags and treated the same as the controlled pollinations. The first five fruit maturing for each cross were collected, weighed, and frozen. The number of drupelets per fruit was determined by counting the number of filled pits in the stored fruit. Percent abortive pollen was determined by counting 400 acetocarmine-stained pollen grains from each of five flowers per replication per clone. Following the harvest season, all plants used in the study were tested for RBDV and TomRSV by ELISA.

The mean fruit weight and drupelet number for each pollination were used in analyzing the data. Data were analyzed as a 4×4 factorial, omitting data for open-pollination, and as a series of one-way analyses of variance using the four pollen parents and open pollination as factors for each female. In addition, the controlled pollination data set was analyzed by general least-squares diallel analysis of variance to estimate general, specific, self, maternal, and reciprocal effects (Schaffer and Usanis, 1969).

Normal 'Centennial' had the lowest percent abortive pollen and crumbly fruited 'Centennial' the highest (Table 1).

Significant maternal, paternal, and maternal × paternal effects for fruit weight and drupelet number occurred (Table 2). The mean squares were slightly larger for paternal than for maternal effects for both fruit weight and drupelet number, and the maternal × paternal interaction was small but significant.

Significant paternal effects on fruit weight were present for normal 'Centennial', 'Chilcotin', and 'Willamette' as females, but not for crumbly 'Centennial' in four one-way analyses of variance (Table 3). Open-pollination and pollen from 'Chilcotin' and 'Willamette' were equally effective for all maternal parents for fruit weight. Pollen from normal and crumbly fruited 'Centennial' generally

Table 3. Effect of paternal (pollen) parent on fruit weight and drupelet numbers for four raspberry clones at Puyallup, Wash., in 1988.

Paternal parent	Maternal parent			
	Crumbly Centennial	Normal Centennial	Chilcotin	Willamette
<i>Fruit weight (g)</i>				
Crumbly Centennial	1.61 a	1.52 c ^z	2.01 c	0.77 c
Normal Centennial	1.27 a	2.92 b	2.35 bc	1.72 b
Chilcotin	1.97 a	4.46 a	3.07 ab	2.80 a
Willamette	2.21 a	4.48 a	3.34 a	3.03 a
Open pollination	1.43 a	3.46 a	3.51 a	2.70 a
<i>Drupelet number</i>				
Crumbly Centennial	24.8 a	29.5 c	36.8 b	21.2 b
Normal Centennial	24.0 a	50.3 bc	38.3 b	30.9 b
Chilcotin	31.8 a	73.2 a	67.1 a	60.4 a
Willamette	40.2 a	64.7 ab	74.2 a	63.1 a
Open pollination	29.2 a	58.8 ab	73.6 a	72.6 a

^zMean separations for each variable within columns by Duncan's multiple range test, $P = 0.05$.

produced smaller fruit than other pollen.

There were significant paternal effects on drupelet number for normal 'Centennial', 'Chilcotin', and 'Willamette' as females, but not for crumbly 'Centennial' (Table 3). Open-pollination and pollen from 'Chilcotin' and 'Willamette' were equally effective for all maternal parents for drupelet number. Pollen from crumbly and normal 'Centennial' produced fewer drupelets for 'Chilcotin' and 'Willamette'. Pollen from crumbly 'Centennial' did not differ from normal 'Centennial' in the number of drupelets produced for any maternal parents.

Results of the diallel analysis (Table 4) supported the previous analysis. General effects and maternal effects predominated, and specific effects were not significant. Self effects were small but significant for fruit weight, but not for drupelet number.

There was no consistent relationship between abortive pollen, as determined by acetocarmine staining (Table 1), and fruit weight and drupelet number (Table 3). Although normal 'Centennial' had a low proportion of abortive pollen, it was a poor pollen parent. Murant et al. (1974) noted that pollen from RBDV-infected plants appeared normal, but was not effective in pollination.

Plants in two of the crumbly fruited 'Centennial' hills and in three of the normal-fruited 'Centennial' hills were found to be infected with RBDV. All 'Chilcotin' and 'Willamette' plants tested RBDV negative. The paternal effects of RBDV were investigated by reanalyzing a subset of the original data using infected and noninfected clones of normal and crumbly 'Centennial' as paternal parents with noninfected 'Chilcotin' and 'Willamette' as maternal parents. Although RBDV-infected 'Centennial' pollen produced smaller fruit (1.65 vs. 1.82 g/fruit, $P = 0.40$) and fewer drupelets (28.9 vs. 36.6 drupelets/fruit, $P = 0.18$) than noninfected pollen, these differences were not significant. Similarly, the maternal effects of RBDV were investigated using the subset of data with 'Chilcotin' and 'Willamette' as paternal parents and infected and noninfected crumbly and normal 'Centennial' as females. RBDV-infected maternal parents produced smaller fruit (2.67 g vs. 3.83 g/fruit, $P = 0.22$) with

fewer drupelets (43.6 vs. 60.6 drupelets/fruit, $P = 0.33$), but these differences were not significant. Therefore, although there may have been maternal and paternal effects of RBDV infection, significant effects could not be demonstrated in this study.

There was no evidence of disease as the cause of the crumbly fruit found in this 'Centennial' clone. All observations were consistent with a somatic mutation as the cause of crumbly fruit in this clone. Although there was a large difference in percent abortive pollen between crumbly and noncrumbly clones of 'Centennial', there was no difference in drupelet set between the 'Centennial' clones when used as paternal parents.

Crumbly fruited 'Centennial' produced small fruit with few drupelets, regardless of the paternal parent. This result suggests that the cause of the crumbly fruit in this clone of 'Centennial' is primarily a maternal effect. There are many factors involved in fruit development that could affect fruit size. These range from pistil number through development of the pistils into drupelets. Although the number of pistils per flower was not counted, there were no obvious differences in pistil number at the time of pollination. There were 50% fewer drupelets per fruit for open-pollinated, crumbly 'Centennial' compared to normal 'Centennial'. A 50% difference in pistil number would have been obvious at the time of pollination. The maternal effect appeared to act at a later stage of development, resulting in drupelet abortion rather than a change in pistil number.

Table 4. Mean squares from diallel analysis of variance of raspberry fruit development at Puyallup, Wash., in 1988.

Source of variation	df	Fruit wt	Drupelet no.
Replication	3	0.89	369
General	3	11.09**	4624**
Specific	2	0.24	218
Self	4	1.65*	343
Maternal	3	8.41**	1685**
Reciprocal	3	1.42*	378*
Error	45	0.46	134

^z***F test of mean-square ratios significant at $P = 0.05$ or 0.01 .

The primarily maternal cause of crumbly fruit in 'Centennial' is in contrast to 'Sumner', where there were both maternal and paternal effects (Daubeny et al., 1967). Although RBDV has been reported to have both maternal and paternal effects on drupelet set (Daubeny et al., 1978; Murrant et al., 1974), these effects were not evident in this study.

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