Reviewed Research Paper

Heterozygosity for Self-incompatibility in Lloyd George Red Raspberry

ELIZABETH KEEP[1]

Since its discovery in a wood in England in 1919, Lloyd George raspberry (*Rubus* idaeus L.) has been the most outstanding and most widely used parent in red raspberry breeding throughout the world. Øydvin (9) reported in 1970 that of the 96 red-fruited raspberry cultivars released since 1930 in the United States, Canada and Western Europe, 32% had Lloyd George as one parent, 37% were more distantly related to Lloyd George, only 31% being unrelated to this cultivar. Lloyd George has been used also in breeding in Eastern Europe, and in Russia sometimes under the name Angliska or Anglijskaja.

Leading varieties derived from Lloyd George include Willamette, Canby, Mecker, and Veten, which are summer fruiting, and Heritage, September and Zeva Herbsternte (fall fruiting). Currently, all the cultivars grown commercially in Britian—Malling Jewel, Malling Delight, Malling Admiral, 'Malling' Leo and Glen Clova – are distantly related to Lloyd George, as are the newer Canadian cultivars Chilcotin, Haida, Matsqui, Nootka and Skeena.

Genetic Investigation of Incompatibility

When self-pollinated, Lloyd George appears to be fully self-fertile with a full set of drupelets, like nearly all red raspberry cultivars. This is in marked contrast to wild forms of the European *R. idaeus vulgatus which* are almost invariably self-incompatible and set very few or no drupelets when self-pollinated (5).

In small scale tests, Keep (5) showed that self-incompatibility in a wild raspberry seedling from the French Alps (selection 767/5, genotype S_1S_2), was inherited according to the multiallelic gametophytic system described by East and Mangelsdorf (2). In this system, incompatibility *S* alleles act independently in the style and inhibit pollen tube growth of pollen carrying like alleles. Self-fertility results from the activity of mutant S_{fert} alleles, pollen carrying such alleles being unaffected by incompatibility alleles in the style. An individual heterozygous for S_{fert} ($S_{fert}S_x$) would be effectively self-fertile since S_{fert} pollen could grow down the style and fertilize both S_{fert} and S_x ovules.

Recently, data showing that Lloyd George is heterozygous for an incompatibility allel, S_5, have been obtained at East Malling from crosses involving a self-incompatible wild raspberry from the French Pyrenees (selection 2503/8). In Family 5309 ((Glen Clova x 2503/8) x Lloyd George) 36 random seedlings were self-pollinated in 1983 or 1984. Twenty-two of these developed a full set of drupelets in all or nearly all fruit pollinated, twelve set very few or no drupelets, while two were graded as intermediate. All 36 produced adequate quantities of pollen and set normally with open pollination.

Assuming Glen Clova is $S_{fert}S_{fert}$, 2503/8 is S_6S_7 and Lloyd George is $S_{fert}S_5$, Family 5309 is ($S_{fert}S_{fert}$ x S_6S_7) x S_{fert} S_5 or $S_{fert}S_{6\text{ or }7}$ x $S_{fert}S_5$ giving the genotypes 1 $S_{fert}S_{fert}$:1 $S_{fert}S_{6\text{ or }7}$: 1 $S_{fert}S_5$: 1 $S_{6\text{ or }7}S_5$. The latter genotype, only, would be self-incompatible, giving an expected ratio of 3 self-fertile : 1 self-sterile.

[1]Fruit Breeding Department, East Malling Research Station, Maidstone, Kent, U.K.

Classing the two intermediate seedlings as self-fertile, the observed ratio of 24 : 12 does not differ significantly from 3 : 1 (X^2 1.33, P 0.3).

LINKAGE RELATIONSHIPS OF THE SELF-INCOMPATIBILITY LOCUS AND ITS EFFECT ON BREEDING BEHAVIOUR

Further evidence indicating that Lloyd George might carry an incompatibility allele was obtained earlier from crossing a yellow-fruited (ttII) Lloyd George derivative with a self-incompatible (S_3S_4) apricot-fruited (*TTii*) wild Russian raspberry selection, 2507/28 (6). Three out of six of the resulting F_1 seedlings proved to be self-incompatible and must have inherited an incompatibility allele from the Lloyd George derivative. It was suggested that a deficit of apricot-fruited seedlings in progenies segregating for the fruit anthocyanin inhibitor gene *i* might have been due to linkage of *i* with the self-incompatibility locus. Keep (6) also suggested that the pollen tube inhibitor gene *w* linked with *t* (yellow fruit) and *g* (pale green leaf) found in Lloyd George and other raspberries (8), might, in fact, be an S incompatibility allele. If this is so, as seems likely, then the incompatibility locus occurs on the only major linkage group so far delineated in *R. idaeus*. This includes amongst others the genes *H* (hairy/glabrous canes), *T*, and *S* (spiny/spineless canes).

These genes are notorious for erratic segregations, reciprocal differences being common and some parental combinations producing normal segregation ratios and others variable deficits or excesses of the recessive class (3, 4, 7). To account for this and for the observed maintenance of heterozygosity for the genes *T* and *H* both in wild populations and breeders' material, Jennings (3) postulated that both genes were each linked with two lethals or semi-lethals in such a way that a balanced lethal system would be present. He suggested that Lewis' gene *w* (8) which he renamed *wt*, might be one such lethal.

An incompatibility allele could well represent one member of Jennings' postulated balanced lethal system. In plants heterozygous for S_{fert}, linked lethals would tend to counter the effects of the competitive advantage of S_{fert} pollen that might occur in, for instance, breeders' material derived in large part from Lloyd George. Such lethals would check the otherwise inevitable tendency towards homozygosity both for S_{fert} and for linked loci such as *T* and *H*. The observed variability in segregations for *T* and *H* (3) could be explained by the effect of incompatibility alleles, in addition to S_5, of varying efficiency, the influence of temperature on the incompatibility system, and, of course, the use of parents homozygous for S_{fert} and/or lacking the postulated linked lethals.

Lloyd George was a selection from the wild and probably resulted from bee pollination of a self-incompatible wild raspberry with pollen of a self-fertile cultivar. Other old varieties of comparable provenance might well have introduced different *S* alleles into breeders' stock. The current interest in wild *R. idaeus* selections as donors in raspberry breeding and their likely combination with, for instance, Lloyd George derivatives (e.g. see (1)) could result in the production of self-incompatible elites. This accentuates the need for pretrial tests for self-fertility.

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Reviewed Research Paper

Quarantined and Quarantine-Released *Prunus* sp. Accessions: The Integration of Quarantined-Germplasm Inventories into the Germplasm Resources Information Network (GRIN)

B. J. PARLIMAN,[1] H. TALBOT,[1] J. D. MOWDER[2] AND N. F. FORAN[1]

Abstract

Prunus genotypes have a quarantine period of approximately 6 to 8 years. The lack of information on what germplasm is currently quarantined has resulted in duplicate orders and difficulties in planning for plant explorations. Elimination of duplication will make all phases of the plant exploration/collection/virus-indexing/distribution system more efficient and effective which means greater availability of new *Prunus* germplasm for breeding and development in the United States. This article briefly reviews plant introduction/quarantine concepts and presents an inventory list of all *Prunus* genotypes currently quarantined at the Glenn Dale Plant Introduction and Quarantine Station. This inventory will be added to the Germplasm Resources Information Network (GRIN) which is a computer-based information system available to users who have a terminal with remote communications capabilities. As a result, all interested researchers will have access to information on *Prunus* that is in the quarantine system or that has been released. This will alter the planning for plant collection trips, will make more effective use of the existing system, will reduce the need for formal and frequent communications among plant introduction/quarantine participants, and will provide for GRIN the skeletal information to which future evaluation and research data can be added.

The Glenn Dale Plant Introduction and Quarantine Station (GDPI/QS) primarily works with vegetatively-propagated germplasm that has been placed in the "prohibited" importation category by Federal regulators (1). Plant genera placed within this category have a high pest risk for U.S. agriculture (4) because they have a high frequency of virus, viroid, and mycoplasma-like organisms (MLO) infections; they may carry new races of fungi or bacteria; and/or originate in countries where high risk pests occur (5). *Citrus, Ipomoea, Malus, Prunus, Pyrus, Rubus,* and *Solanum* sp. are among the most important and frequently quarantined crop plants processed at GDPI/QS.

U.S. Department of Agriculture, Agricultural Research Service, Plant Genetics and Germplasm Institute, [1]U.S. Plant Introduction Station, Glenn Dale, MD, 20769-9157, and [2]GRIN Database Management Unit, Beltsville Agricultural Research Center-West, Beltsville, MD 20705-0811.

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