J. Amer. Soc. Hort. Sci. 119(6):1289–1292. 1994.

A Mutation in 'Nonpareil' Almond Conferring Unilateral Incompatibility

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Additional index words. Prunus dulcis, Prunus amygdalus, breeding, pollination

Abstract. **'Jeffries', a mutant of 'Nonpareil' almond [*Prunus dulcis* (Mill.) D.A. Webb], showed "unilateral incompatibility" in that its pollen failed to fertilize cultivars in the 'Carmel' (CIG-V), 'Monterey' (CIG-VI), and 'Sonora' (CIG-VII) pollen cross-incompatibility groups (CIGs), as well as specific cultivars ('Butte', 'Grace', and 'Valenta') whose CIG group is unknown. 'Jeffries' is not self-compatible, but produced good set when pollinated by 12 almond cultivars representing the entire range of CIGs involving 'Nonpareil' parentage, as well as the parent 'Nonpareil'. It was concluded that the 'Jeffries' mutant—both gametophyte and sporophyte—expressed a loss of a single *S* allele of the 'Nonpareil' genotype.**

Almond shows self-incompatibility (SI) of the gametophytic type (Socias y Company, 1991). In commercial orchards, cross-compatible cultivars are planted in alternate rows to provide cross-pollination (Tufts, 1919; Tufts and Philp, 1922). 'Nonpareil' is the most important almond cultivar in California (Asai et al., 1994). Standard pollinizers include 'Carmel', 'Fritz', 'Price', 'Merced', 'Sonora', and 'Monterey'. Seven reciprocally cross-incompatible groups (CIGs) have been identified among California cultivars (Kester et al., 1994) (Table 1).

'Jeffries', a patented cultivar that originated as a mutation of 'Nonpareil', was discovered as a high yielding limb in a 'Nonpareil' orchard where no other cultivar had been provided for cross-pollination. Except for the purported high productivity, the cultivar is identical to 'Nonpareil' in tree and nut characteristics. However, when 'Jeffries' trees were planted with 'Carmel' pollinizers in commercial orchards as a substitute for 'Nonpareil' in standard 1:1 plantings, good crops were produced on 'Jeffries' but poor crops were produced on the adjoining 'Carmel' pollinizer. On the other hand, good crops were produced by both 'Fritz' and 'Jeffries' trees when these two cultivars were planted together in a standard 1:1 combination. The problem was hypothesized to be an example of "unilateral incompatibility" between 'Carmel' and 'Jeffries'.

In this paper we present results of an investigation to confirm the apparent "unilateral incompatibility" between 'Carmel' and 'Jeffries' and to test the incompatibility relationships between 'Jeffries' and a range of almond cultivars representing differing CIGs.

Received for publication 28 Feb. 1994. Accepted for publication 2 May 1994. Partial support for this project was provided by the Almond Board of California, Sacramento. Assistance in carrying out the project was provided by Richard N. Asay, Jim Yeager, and Karen Pelletreau. Acknowledgement is made to Jerry Wilson and Ron and Karen Weins, Bakersfield, Calif., in whose orchards some of the tests were conducted. Use of trade names implies neither endorsements of the products named nor criticisms of similar ones not named. Conversations pertaining to this project with R. Socias y Company, and Wm. Burchell are acknowledged as well as reviews of the manuscript by T. Gradziel, Dan Parfitt, and Vito Polito. 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.
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Materials and Methods

In 1984, flowers and percent nut set [number of nuts set/number of flowers pollinated) were counted on open-pollinated branches in 'Carmel'–'Jeffries' and 'Carmel'–'Fritz' combinations in the Wilson and Weins orchards in the southern San Joaquin valley of California, where the problem was occurring. Similar counts were made on comparable trees of 'Nonpareil' in a nearby (Anderson) orchard. Ten and eleven replications of ≈200 each blossoms were used.

Hand-pollination tests were conducted in three commercial orchards in Kern Co., where the problem was occurring. Pollen of 'Jeffries', 'Carmel', and 'Fritz' were collected from trees of the same orchards. 'Nonpareil' and 'Merced' pollen was collected from trees in Kern Co., where a cultivar collection was maintained. In 1985, pollen was collected from 'Jeffries' trees in the Wilson and Weins orchards. Pollen of 'Nonpareil' and a series of other cultivars was collected from the Delta College Regional Variety Plot, Manteca, Calif.

In 1984, blossoms were emasculated just before anthesis. Pollen was applied directly to the stigmas with a glass rod. Three unbagged replications of ≈100 blossoms were used for each test. An equal number of emasculated but unpollinated blossoms was left as a check. In 1985, the blossoms were unemasculated but limbs were covered with tight mesh bags before bloom opening to prevent bee visits. Pollen was applied directly to the stigmas immediately after the flowers opened. Two to four enclosed limbs of ≈100 flowers each were used for each test. An equal number of bagged but unpollinated blossoms was included as a check.

Pollen germination was tested by growing on 20% sucrose agar solution and observing pollen tube growth under a dissecting

Table 1. Cross-incompatibility groups for California almond cultivars.

Group	Cultivars
CIG–I	Nonpareil, I.X.L., Long IXL, Profuse, Tardy Nonpareil
CIG–II	Mission, Ballico, Languedoc
CIG–II	Thompson, Robson, Harvey, Granada, Sauret #2, Mono, Wood Colony
CIG–IV	Merced, Ne Plus Ultra, Price Cluster, Norman, Ripon, Rosetta
CIG–V	Carmel, Carrion, Sauret #1, Livingston, Monarch
CIG–VI	Monterey, Seedling 1–98
CIG–VII	Sonora, Vesta, Solano, Kapareil

microscope. Observations were also made for staining after treatment of pollen with acetocarmine.

Trees at the Regional Variety Trial (RVT) plot at Manteca, Calif., as well as in the Univ. of California, Davis, experimental orchards were used for crosses of 'Jeffries' with 'Nonpareil' pollen. Reciprocal crosses on 'Jeffries' with pollen from different cultivars were made in commercial orchards.

Results

First-year results. 1984. Percent sets from open-pollination (Table 2) of 'Jeffries' were significantly higher (two to four times) than 'Carmel' in adjoining rows of the same orchards. Set on 'Fritz' was significantly higher than on 'Carmel' in adjoining trees of the same orchard, the same as 'Jeffries' in the other two orchards, and the same as 'Nonpareil' in a nearby orchard. These results confirm that a yield problem was occurring in 'Carmel' with 'Jeffries' as a pollinizer.

Controlled hand-pollinated crosses confirmed that 'Jeffries' pollen produced very low percentage nut set on 'Carmel' (Table 3) in contrast to the high percentage sets produced by 'Nonpareil' and 'Fritz' pollen. On the other hand, 'Nonpareil', 'Carmel', and 'Fritz' pollen produced equally high percent nut set on 'Jeffries' trees. 'Merced' pollen produced low sets on all trees tested.

In pollen viability tests, 'Jeffries' pollen germinated well (≥70%) and stainability was also high, indicating that poor pollen viability was not the problem. Furthermore, high percent sets resulted when this same pollen was used on other cultivars. In contrast, pollen of 'Merced' germinated poorly (≤10%), contained numerous shriveled pollen grains, and produced low set on each tree where it was used for pollination. Thus, set in 'Merced' in 1984 was attributed to poor quality pollen and not to incompatibility relationships.

Controlled hand-pollination tests with 'Jeffries' pollen also produced low percentage sets on 'Carmel' trees at the RVT Manteca plot (Table 4), thus confirming the results obtained at the Weins and Wilson orchards. These values were not significantly different from those produced by the unpollinated check. On the other hand, pollen of both 'Nonpareil' and 'Carmel' produced high percentage set. 'Merced' pollen produced low sets.

Second-year results. 1985. Pollination tests confirmed the unilateral incompatibility relationship between 'Jeffries' and both 'Nonpareil' and 'Carmel' and extended this relationship to other members of the 'Carmel' CIG, including 'Carrion' and 'Sauret No. 1' (Table 5). Similarly, unilateral incompatibility occurred between 'Jeffries' and 'Solano', 'Sonora', 'Monterey', and 'Butte'. On the other hand, reciprocal cross-incompatibility was not observed between 'Jeffries' and 'Merced', 'Thompson', 'Sauret No. 2', 'Fritz', or 'Peerless'. 'Merced' pollen in 1985 was highly viable and resulted in good set. 'Sauret #1' was identified as reciprocally incompatible with 'Jeffries' and is also in CIG-V. 'Monterey' is in CIG-VI and was identified as reciprocally incompatible.

Table 2. Nut set produced by open pollination in commercial almond orchards in Kern Co. (Calif.) in 1984.

Orchard	Cultivar	Branches (no.)	Nut set (%)	Significance[z]
Wilson (1)	Jeffries	10	24.4	B
	Fritz	11	41.0	A
(2)	Jeffries	11	38.0	A
	Carmel	10	8.1	C
Wein	Jeffries	10	38.6	A
	Carmel	10	19.3	B
Anderson	Nonpareil	10	45.7	A

[z]Analysis of variance. Duncan's multiple range test. Different letters indicate significance at $P = 0.05$.

Table 3. Nut set produced by controlled crosses in problem almond orchards in Kern Co. (Calif.) in 1984.

Orchard	Seed parent	Pollen parent	Nut set[z] (%)
Wein	Carmel	Nonpareil	42.9*
		Fritz	35.5*
		Jeffries	4.0
		Merced	3.0
		Unpollinated check	1.3
	Jeffries	Nonpareil	39.0*
		Carmel	34.2*
		Fritz	24.6*
		Merced	6.0
		Unpollinated check	1.3
Wilson	Fritz	Carmel	45.1*
		Jeffries	36.8*
		Nonpareil	35.2*
		Merced	16.5
		Unpollinated check	7.2
	Jeffries	Carmel	49.9*
		Nonpareil	42.2*
		Fritz	38.2*
		Merced	5.7
		Unpollinated check	2.0

[z]Means of three branches. Analysis of variance. Duncan's multiple range test.
*Significantly different from unpollinated check at $P = 0.01$.

Table 4. Nut set on 'Carmel' almond trees produced after cross-pollination with pollen of different sources. RVT Manteca plot. 1984.

Pollen parent	Source	Nut set[z] (%)
Fritz		43.2*
Nonpareil		23.3*
Nonpareil		20.5*
Merced		3.4
Jeffries	Wilson	1.8
Jeffries	Wilson	0.4
Jeffries	Wein	0.2
Unpollinated check		1.4

[z]Analysis of variance. Duncan's multiple range test.
*Significantly different from unpollinated check at $P = 0.01$.

Results in 1986. In 1986, limited screenings were made to compare crosses of pollen from 'Jeffries' and 'Nonpareil' on a wider range of cultivars of known and unknown CIGs (Table 6). The tests consisted of a single branch of ≈100 blossoms of each pollen type on trees of eleven cultivars. Four cultivars showed unilateral incompatibility. The CIGs for 'Grace' and 'Valenta' are unknown, but these cultivars appear to share the same S-allele associated with the unilateral incompatibility in 'Jeffries'. The remaining seven cultivars did not show unilateral incompatibility. 'Woods Colony' showed lower percent set with 'Carmel' pollen than 'Nonpareil', but the level was still relatively high. This cultivar has been previously identified with CIG-III and should not show unilateral incompatibility.

Discussion

'Mission' and 'Nonpareil' have been shown to have combinations of S alleles which have been designated as S_aS_b and S_cS_d,

Table 5. Tests for reciprocal incompatibility of 'Jeffries' with almond cultivars of different CIGs.

		Jeffries			Nonpareil
Cultivar	CIG	Seed parent (%)	Pollen parent (%)	Unpollinated check (%)	seed parent (%)
Nonpareil	I	11.5*	3.3	0.0	0.0
Mission	II	48.0*	13.25*	5.5	48.0*
Sauret #2	III	45.0*	29.75*	5.0	67.5*
Merced	IV	nt[z]	61.0*	0.0	66.0*
Carmel	V	34.25*	1.5	1.0	30.0*
Carrion	V	30.0*	1.5	0.0	20.0*
Sauret #1	V	34.0*	5.0	1.5	66.5*
Monterey	VI	29.5*	7.5	5.0	25.0*
Sonora	VII	nt	7.5	5.5	48.0*
Solano	VII	28.25*	0.0	2.0	9.5*
Butte	Unknown	33.25*	8.0	5.5	19.5*
Fritz	Unknown	26.25*	73.0*	4.3	70.0*
Peerless	Unknown	36.0*	77.0*	2.0	37.0*

[z]nt = Not tested.
*Significantly different from the unpollinated check at $P = 0.01$.

Table 6. Screening of different almond cultivars for 'Jeffries'–'Nonpareil' CIG relationships. 1989. Single tests of ≈100 flowers.

		Pollen parent	
Seed parent	CIG group	Jeffries (%)	Nonpareil (%)
I. Unilaterally incompatible			
Sauret #1	V	7	12
Monarch	V	6	16
Grace	Unknown	0	28
Valenta	Unknown	8	72
II. Not unilaterally incompatible			
Woods Colony	IV	18	29
Aldrich	Unknown	30	28
Dottie Won	Unknown	27	28
Padre	Unknown	66	62
Pearl	Unknown	52	78
Ruby	Unknown	53	12
Tokyo	Unknown	12	6

respectively. The four CIGs representing the four possible progeny combinations have been identified and their genotypes designated (Table 1) along with CIG-VII resulting from 'Nonpareil' and 'Eureka' parentage (Kester et al., 1994). Of the CIG groups tested, S_d is the only allele common to 'Nonpareil', 'Carmel', and 'Monterey', all of which show unilateral incompatibility with 'Jeffries'. It was concluded that 'Jeffries' pollen had a genotype with only one effective S allele. Crossa-Raynaud and Grasselly (1985) have assigned the genotype designation S_7S_8 to 'Nonpareil'. Assuming that the S_7 allele is not present or not functioning, S_8 is the only S allele present either in a homozyous (S_8S_8) or a heterozyous (S_8S_x or $S_8S\_$) state. Under these conditions, 'Jeffries' pollen would not function in a style of any cultivar with the S_8 allele in its genotype. On the other hand, any genotype with two different S alleles, including the unilaterally incompatible cultivars, should be able to pollinate and fertilize 'Jeffries', since at least one S allele would always be different. Pollen from 12 different cultivars covering the range of incompatibility groups identified so far produced compatible reactions (Table 5).

Progeny tests with 'Nonpareil' pollen (or any other with an S_8 allele) and 'Jeffries' should provide an answer to the single allele hypothesis in that only S_7S_8 genotype seedlings would be produced, all incompatible with the pollen parent. In contrast, a cross with a genotype without S_8 alleles would provide two genotype classes, both compatible with the pollen parent but reciprocally incompatible with 'Jeffries'.

The 'Jeffries' mutant is different from the self-compatible mutants represented by the 'Stella' cherry cultivar (Lapins, 1970) and 'Supernova' mutant (Monastra et al., 1987) of 'Fascionello' almond, both produced by irradiation. Their self-compatibility apparently results from a change in the "recognition" mechanism of the incompatibility genes. This situation does not occur in the 'Jeffries' mutant because 'Jeffries' pollen does not appear to function in the 'Jeffries' style.

On the other hand, the ability of 'Nonpareil' pollen to function in the 'Jeffries' styles provides an opportunity to self-fertilize an otherwise self-incompatible 'Nonpareil' genotype. This capability provides for interesting genetic possibilities in exploring the genetic potential of 'Nonpareil', which is the leading almond cultivar in California and has been utilized as a parent in many crosses (Gradziel, 1992).

The 'Jeffries' mutant should be a useful marker in genetic and origin studies. One could test large numbers of cultivars for the presence of the S_8 allele. In the California genepool (Hauagge et al., 1987), presence of the S_8 allele provides evidence of 'Nonpareil' parentage. 'Nonpareil' and 'Mission' are the putative parents of members of the 'Carmel' and 'Monterey' incompatibility groups. Crossing between 'Nonpareil' and 'Eureka' gave rise to the 'Sonora' group. On the other hand, 'Butte' apparently has an S_8 allele but has not been identified as one of the four groups of the 'Nonpareil' x 'Mission' family. This cultivar may be a seedling from 'Nonpareil' crossed with some cultivar other than 'Mission'. 'Fritz' and 'Peerless' represent different CIGs whose identities have not been determined.

Genotypes can be screened rapidly for presence of S_8 by pollinating them with 'Jeffries' pollen. Ideally, unilateral incompatibility should be evaluated by comparing the reciprocal crosses by also applying pollen to 'Jeffries' styles. Given the universal compatibility of any cultivar with 'Jeffries' styles, the information gained by the extra effort would not be worthwhile in a preliminary screen.

Test crosses with 'Jeffries' and 'Nonpareil' in 1986 extended the range of cultivars with the putative S_8 allele (Table 6) to include 'Grace', and 'Valenta', whose CIG is otherwise unknown. These two cultivars are likely to have 'Nonpareil' as one of the parents crossed with a cultivar different from 'Mission'. 'Monarch' is in the 'Carmel' CIG and 'Sauret #1' and 'Woods Colony' are in the 'Thompson' group. Similarly, the CIG for 'Aldrich', 'Dotty Won', 'Padre', 'Pearl', 'Ruby', and 'Tokyo' are unknown but do not have the S_8 allele.

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